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Incidence of a Parasitic Ascarid, *Porrocaecum decipiens*, in the Common Porpoise, *Phocoena phocoena*, from the Lower Bay of Fundy¹

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ABSTRACT

Examinations were made of nematodes from the stomachs of 150 common porpoises (*Phocoena phocoena*) collected from 1952 to 1956 from the lower Bay of Fundy, one common porpoise from St. Ann's Bay, Nova Scotia, and one white whale, (*Delphinapterus leucas*) from Mace's Bay, New Brunswick.

One adult *Porrocaecum* was found. Larval *Porrocaecum* in numbers ranging from 1 to 21 were found in about 25% of 50 porpoise stomachs collected in 1955 and 1956. Eighty larval *Porrocaecum* were present in the stomach of the white whale. No trace of reproductive organs was observed in any of the larval *Porrocaecum*.

It is concluded that the common porpoise in the lower Bay of Fundy is not an important host of adult *P. decipiens*.

INTRODUCTION

SINCE 1946 the stomachs of several species of predators on marine teleosts have been examined for adults of the parasitic ascarid, *Porrocaecum decipiens*. The larvae of this nematode are common in fillets of Atlantic cod (*Gadus callarias*) and other fishes in east-coast Canadian waters. Because adult *P. decipiens* have been found in the stomach of the common porpoise (*Phocoena phocoena*) in the Baltic Sea by Schmidt-Ries (1939), it was thought that this widespread cetacean might also be a definitive host of *P. decipiens* in Canadian waters. This paper presents the results of an examination of nematodes from the stomachs of about 150 common porpoises and one white whale (*Delphinapterus leucas*).

MATERIALS

Throughout this account the terms "larvae" and "larval" are used to denote nematodes which lacked any trace of reproductive organs. Because of the absence of diagnostic specific characters in larvae of the genus *Porrocaecum*, we refer to these larval worms as *Porrocaecum*. Evidence that the majority of larval *Porrocaecum* in these waters are *P. decipiens* has been adduced by Scott (1956).

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Nematodes were collected from the stomachs of 150 immature and adult common porpoises killed with one exception in the area immediately outside the entrance to Passamaquoddy Bay in the lower Bay of Fundy. This area is noted for the high incidence of *P. decipiens* in fish (Scott and Martin, 1957). All were collected in the months of May to November over a five-year period from 1952 to 1956. The intestines of 2 common porpoises from this area were also examined. One stomach was collected from a common porpoise taken at St. Ann's Bay, Cape Breton Island, in August, 1950. The nematodes from a stomach of a white whale captured in June, 1952, at Mace's Bay, New Brunswick, on the Bay of Fundy were also available for study.

Fisher counted the nematodes from the stomachs of about 100 porpoises collected from 1952 to 1954. Identifications of all nematodes in these collections were not made. Only the largest nematodes were examined by Fisher, who considered that the other nematodes were too small to be identified or to be mature. Because of this selection it is likely that, although all adult nematodes were probably found, some larval *Porrocaecum* were not examined.

The remaining collections of nematodes including that from the porpoise from St. Ann's Bay and that from the white whale were examined by Scott. In these collections, all nematodes were counted; each was examined and, where possible, was identified to genus. All *Porrocaecum* identified by Scott were dissected under a binocular microscope to determine the state of sexual maturity. These were compared with 20 larval *Porrocaecum* taken from fillets of Atlantic cod. They were also compared with 20 *Porrocaecum* recovered from the stomachs of young harbour seals (*Phoca vitulina*) 3 to 6 days following the experimental introduction of larval *Porrocaecum* into seals (Scott, 1953).

INCIDENCE OF NEMATODES

The results of our examinations are summarized in the accompanying Table.

All nematodes identified as *Porrocaecum* were larvae except for one in 1954 which was judged to be a male by Fisher. A definitive identification of this specimen was not made. The incidence of larval *Porrocaecum* was low. Small numbers, ranging from 1 to 21, were found in about 25% of the stomachs collected in 1955 and 1956. *Porrocaecum* was present in porpoise stomachs from May to

TABLE I. Incidence of nematodes in 150 stomachs of the common porpoise (*Phocoena phocoena*) collected near Passamaquoddy Bay, Bay of Fundy, from 1952 to 1956.

	1952	1953	1954	1955	1956
Number of stomachs	31	9	59	30	21
Stomachs with nematodes	9	0	12	17	16
Stomachs with <i>Porrocaecum</i>	a	0	a	7	6
Mean number of nematodes per stomach	7	0	2	7	13
Mean number of <i>Porrocaecum</i> per stomach	a	0	a	0.6	0.8
Total number of adult nematodes	1	0	1	2	3
Total number of adult <i>Porrocaecum</i>	0	0	1	0	0

^aIdentification of small nematodes was not complete in 1952-54. Larval *Porrocaecum* were present in at least one stomach in 1952 and in one in 1954.

September but was not found in 5 stomachs collected in October, 1954, or in one collected in November, 1955.

Nematodes of other genera, provisionally identified as *Anisakis* and *Contracaecum*, were several times as common as *Porrocaecum*. Most were larval nematodes; only 5 adult nematodes were found. Three of the adults were *Anisakis* and two were *Contracaecum*.

There were 19 nematodes, all larvae of *Anisakis* or *Contracaecum*, in the stomach of the porpoise from St. Ann's Bay.

The larval *Porrocaecum* from porpoises showed no difference from a sample of 20 larval *Porrocaecum* from cod filets. The lips of the nematodes in each group showed the typical larval condition. The *Porrocaecum* from porpoises were much more immature than those recovered 3 to 6 days following their experimental introduction into young harbour seals. None of the *Porrocaecum* from porpoises showed any trace of reproductive organs.

No nematodes were found in the intestines of two porpoises.

In the stomach of the white whale 507 nematodes were found. None was an adult *P. decipiens*; 80 were larval *Porrocaecum*. Most of the *Porrocaecum* had typical larval lips but 16 appeared slightly more developed in that the appearance of their lips approximated to the appearance of the lips in the larval *Porrocaecum* from seals. The remaining nematodes were referred to the genus *Anisakis*. About 50% of the *Anisakis* appeared to be sexually mature.

DISCUSSION AND CONCLUSION

Our observations that adult ascarids were very rare in the common porpoise contrast sharply with those of Schmidt-Ries (1939). In 2 stomachs of the common porpoise from the Baltic Sea that he examined, Schmidt-Ries found that adult *P. decipiens* was the most abundant of 3 species of adult ascarids. The only other species recorded by Schmidt-Ries were *Anisakis typica* and *A. simplex*. Schmidt-Ries, unfortunately, did not state the number of ascarids examined.

It is difficult to account for these striking differences. In the Passamaquoddy Bay area high incidences of larval *Porrocaecum* in cod and high incidences of adult *P. decipiens* in harbour seals have been recorded respectively by Scott and Martin (1957) and by Scott and Fisher (1958). *A priori*, the common porpoise in the Passamaquoddy Bay area, since some of the fishes upon which it feeds are hosts of larval *Porrocaecum*, should also be infected with adult *P. decipiens*. It is clear, however, from our results that such is not the case. It is possible that the porpoises had not been in the area long enough for newly-ingested nematodes to complete their development. This explanation seems implausible because field observations by Fisher (Sergeant and Fisher, 1957) indicate clearly that the common porpoise is numerous along the New Brunswick shore of the lower Bay of Fundy from the end of June to the end of September. It is likely then that we are dealing with a population of porpoises that is continuously exposed to infection by larval *Porrocaecum* and other ascarids. If this is the case, then the absence of adult *P. decipiens* and the scarcity of other ascarids probably results from the failure of the larval ascarids to develop to maturity.

The marked immaturity of all the larval *Porrocaecum* from our collections and the fact that they were found in porpoises in most months of the 5 years for which we have records support the latter idea. At present, however, the only justifiable conclusion is that there is no evidence that the common porpoise in the Passamaquoddy Bay area in the summer is an important host for adult *P. decipiens*.

The foregoing conclusion is based mainly on the scarcity of adult *P. decipiens* in the stomachs of porpoises. Adult *P. decipiens* may possibly occur in the intestines, but their absence in the two intestines examined by us does not support this idea. Moreover, the fact that Schmidt-Ries found adult *P. decipiens* in the stomachs indicates that we were justified in largely confining our observations to the nematodes from the stomachs.

The absence of *P. decipiens* from the porpoise from St. Ann's Bay, another region of high incidence of larval *Porrocaecum* in cod, suggests that our conclusion may apply generally to the common porpoise throughout the east-coast area.

The absence of adult *P. decipiens* and the presence of many larval and adult *Anisakis* in our single specimen of the white whale agree generally with the findings of Vladykov (1944) on white whales in the Gulf of St. Lawrence. Unlike Vladykov, we found larval *Porrocaecum*. A few of these appeared to have developed slightly beyond the larval stage of the worm as it appears in fish. Since the white whale occurs only rarely in the Bay of Fundy (Sergeant and Fisher, 1957) our specimen may have just moved into the area shortly before it was captured. Accordingly, there would have been insufficient time for recently-ingested *Porrocaecum* to become mature. Our evidence does not, therefore, rule out the possibility that white whales may be definitive hosts of *P. decipiens*.

ACKNOWLEDGMENT

Mr. Vinton Leavitt, Back Bay, N.B., collected most of the porpoises examined by us. It is a pleasure to acknowledge his assistance.

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The Abundance and Distribution of the Northern Sea Lion (*Eumetopias jubata*) on the Coast of British Columbia¹

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ABSTRACT

The abundance and distribution of the northern sea lion, *Eumetopias jubata*, in British Columbia are described chiefly on the basis of a survey conducted during the summer of 1956. Results of surveys and censuses made in the years 1913, 1916, 1938 and 1955 are included for comparison. Most major rookeries and hauling-out sites were visited in 1956. Some which were missed were surveyed by aircraft in 1957.

The numbers of sea lions in British Columbia are estimated to be 11,000–12,000 in 1956–57. They have apparently changed little since 1913 and 1916 when the population is estimated less reliably to have been 12,000–13,000. Some changes have occurred in their distribution, mainly as a result of organized destruction of concentrations centred near to fishing areas. Numbers in the Sea Otter Group have been reduced to about one-quarter of their former abundance. Numbers on the Cape St. James rookery, where the population has seldom been molested, have doubled.

Present rookeries include: Triangle, Sartine, and Beresford Islands, in the Scott Island group; Kerouard Islands off Cape St. James; and North Danger Rocks. The Virgin and Pearl Rocks in the Sea Otter Group are no longer rookeries. Sartine Island and North Danger Rocks are recorded for the first time as rookeries. The Scott Islands and Kerouard Islands rookeries accommodate approximately 70% of the entire population, and 90% of the pups during the summer breeding season.

Destruction of approximately 1,000 sea lions annually, when many of these are pups, is shown to be ineffective in substantially reducing the total population. Where efforts are concentrated in one area such as the Sea Otter Group, however, a local population can be greatly reduced and pupping curtailed or stopped.

Pups are born from late May until late June. Soon after giving birth, the cows are serviced by the harem bulls. The harem structure, which averages about 10 cows per harem bull on the rookeries, begins to disintegrate near the end of July when pups take to the water and dominant bulls are replaced by reserve bulls. Some cows, probably not more than 25% at any one time, may forgo the normal annual pregnancy and continue to nurse a pup for more than a year.

It is calculated that more than 70% of the sexually mature females in this population are pregnant in any one year. Natural mortality among the pups appears to be slight, but severe storms in some years may cause heavy pup mortality and constitute an important check on population growth.

INTRODUCTION

THE NORTHERN SEA LION has been accorded some prominence in the fauna of British Columbia by reason of its reputation for destroying commercially valuable fish and fishing gear. Numerically, its numbers are not large. Throughout its North American range, which extends from the islands of southern California northward along the coast into the Bering Sea, it is estimated to number about 60,000 animals (Kenyon and Scheffer, 1953). This report describes the numbers of sea lions and their distribution in Canadian waters. The work was carried

¹Received for publication August 23, 1957.

out during the summer of 1956 and forms a basic part of a more extensive study of the life history, population dynamics, and feeding habits of the species.

In consequence of complaints that sea lions were seriously damaging important commercial fisheries, an investigation of the numbers and locations of sea lions frequenting and breeding along the coast of British Columbia was conducted in the spring of 1913 (Newcombe and Newcombe, 1914). A commission from the Biological Board of Canada was appointed in 1915 to inquire into the effect of a federal bounty offered as an aid to the reduction of sea lions in British Columbia (Newcombe, Greenwood and Fraser, 1918). The work of 1915, which considers sea lions mainly as they relate to alleged damage to the fishing industry, was continued in 1916 with an estimate of numbers in major breeding areas.

The British Columbia Fisheries Commission of 1922 recommended that



FIGURE 1. Major locations of sea lions in British Columbia during the summer breeding season.

patrol vessels attempt to reduce the population on the rookeries near the mouth of Rivers Inlet. Almost every year since this time the Department of Fisheries has destroyed sea lions on these rookeries and in other localities in the Province (Table V). As part of its programme to alleviate the problem of sea lion damage the Department of Fisheries made counts of numbers in 1938, 1955 and 1956.

The 1956 census includes counts made during the course of four separate expeditions. The first, during the last week of May, was to the Sea Otter Group, the Scott Islands, and Solander Island; the second, during the second week in June, to Beresford Island; the third, during the last week in June and the first week in July, to the Scott Islands; and the last, from mid-July on through the first week in August, to all major rookeries and the west coast of Banks Island. Locations of these rookeries and hauling-out sites are shown in Figure 1. The areas covered included all previously known rookeries and most other locations where concentrations of sea lions had been reported. The 1956 census did not cover some localities in the vicinity of the Queen Charlotte Islands. These were surveyed from the air in July, 1957 and the resulting data on numbers and distribution included in this report.

METHODS OF INVESTIGATION

All known rookeries and summer hauling-out sites, with the exception of the aforementioned localities in the Queen Charlotte Islands, were visited at least once during the 1956 summer breeding season. Counts were made using "hand tally counters". Usually two observers made counts independently and simultaneously. Results of the two counts were usually well within 5% agreement for small populations and 10% for large populations. Estimates recorded for each site are a compromise between the two counts. These are considered to be reliable within a 10% error. Bonnet and Ripley (1948) found that estimates of sea lion numbers agreed within 5% with actual counts made from aerial photographs.

Counts were made whenever possible from shore and at close range. In some instances it was not possible to effect a landing, so counts were made from aboard ship with the aid of binoculars. Where populations were small, all individuals were counted. Where populations were large and densely crowded, the total number was estimated with reference to a sample group. Sea lions will sometimes take to the water when disturbed, but during the breeding season they usually remain in groups near to the shore in rookery locations and are not difficult to count.

Supplementary data on numbers and distribution in the vicinity of the Queen Charlotte Islands were obtained during an aerial survey conducted in July, 1957. A "Beaver" aircraft flying at a height of 500 feet was used. Aerial photographs were taken for detailed study of individual size and sex components in each colony and for checking on direct counts.

Figures for the 1938, 1955, and 1956 counts made by Fisheries Officers are taken from files of the Department of Fisheries in Vancouver.

RESULTS

Results of sea lion counts on major rookeries and summer hauling-out grounds are tabulated in Tables I, II, and III. Newborn pups are recorded separately from older animals which are termed "adults" as a matter of convenience. The term "adult" includes a substantial number of adolescents and other non-breeders.

TABLE I. Numbers of sea lions counted on Scott Islands.

1. Triangle Island								
Year Month Day	1913 July 15, 19	1916 June 26	1938 Aug. 19	1956 May 27	1956 July 7	1956 Aug. 1	1956 Aug. 14-18	
Adults	250	"none breeding"	—	650*	700	1,350		
Pups	50	"none breeding"	—	none seen	300	400		
Total	300	—	1,200	650	1,000	1,750	315**	
2. Sartine Island								
Year Month Day	1913 July 15, 19	1916 June 26	1938 Aug. 19	1956 May 27	1956 July 7	1956 Aug. 1	1956 Aug. 14-18	
Adults	none seen	none seen	2	100*	550	350		
Pups	none seen	none seen	—	none seen	—*	300		
Total	—	—	—	100	550	650	675**	
3. Beresford Island								
Year Month Day	1913 Aug. 17, 25	1916 June 26	1938 Aug. 19	1956 May 27	1956 June 9, 10	1956 July 1, 4	1956 July 31	1956 Aug. 14-18
Adults	2,500	—	—	700*	1,000	950	550	
Pups	700	—	—	only 1 seen	450	750	350	
Total	3,200	6,000	2,000	700	1,450	1,700	900	975**

*Sea conditions did not permit close observation. **Including pups.

TABLE II. Numbers of sea lions counted at Sea Otter Group

1. Virgin Rocks							
Year Month Day	1913 Aug./Sept. 28, 29/2	1916 June 25	1938 Aug. 19	1956 May 25	1956 July 17	1956 Aug. 14-18	
Adults	2,300	1,500	—	370	370	—	
Pups	1,000	1,000	—	none seen	none seen	—	
Total	3,300	2,500	4,000	370	370	700	
2. Pearl Rocks							
Year Month Day	1913 June 21	1913 Aug. 29	1916 June 25	1956 May 25	1956 July 17	1956 Aug. 14-18	
Adults	1,050	—	200	300	200	—	
Pups	300	—	50	none seen	none seen	—	
Total	1,350	500	250	300	200	200	

TABLE III. Numbers of sea lions counted near Cape St. James and North Danger Rocks.

1. Cape St. James and Kerouard Islands						
Year Month Day	1913 June 12, 13	1916 July 13	1938 Aug. 16	1955 Sept. 12	1956 July 25	1956 Aug. 14-18
Adults	—	—	—	—	2,500	—
Pups	—	—	—	—	1,500	—
Total	2,000*	1,000*	2,800	4,500	4,000	4,500*

2. North Danger Rocks					
Year Month Day	1938 Aug. 17	1955 Aug. 14	1956 July 18	1956 Aug. 14-18	
Adults	—	—	800		
Pups	—	—	300		
Total	2,000	600	1,100	550	

*Including pups.

Few sea lions are found at sea or far removed from rookery sites during the breeding season. Only rarely did they appear far from shore although many miles of open sea were searched. The combined total numbers counted during the summer months on the Scott Islands, Virgin and Pearl Rocks, North Danger Rocks and Kerouard Islands are estimated at 80% or more of the entire population.

Some changes occur in the numbers of sea lions on the rookeries as the breeding season advances. Observations were not started until the last week in May, so it is not known at what time the bulls take up their territories and commence to acquire harems. Harem groups dominated by attendant bulls are present during the last week in May. Pupping commences about this time. On May 27, only one pup, which had just been born, was observed. On Beresford Island pups comprised 31% of the entire count on June 9 and 10. On July 1 and 4, in this same locality, pups comprised 43% of the entire count, and almost every cow was accompanied by a pup. Mating was in progress during the first week in July. A change in the breeding structure had occurred by July 31. Cows and pups were located near to the water at this time and pups were generally congregated in groups with few or no cows in attendance. Large bulls appeared to have diminished in numbers, but younger bulls were present in greater numbers. Most cows had apparently been serviced by this time as suggested by their behaviour in spurning the advances of the bulls. The harem structure had almost entirely disintegrated and many animals, both male and female, had apparently left the rookeries. The first week in July is, therefore, the best time to make counts, as a maximum number of animals are present on the rookeries at this time.

The Scott Islands comprise a string of five islands and associated rocks located northeast of Cape Scott near the northern tip of Vancouver Island. Triangle Island, the outermost of the group, is located 26 nautical miles from Cape Scott. Rocks and small islets surrounding the island provide many suitable

hauling-out grounds for sea lions. The largest single group, a rookery, was located off the north end of the island. Another large colony was located on several small rocks stretching about a mile to the northeast. No pups were seen in this colony. A second small rookery is located off the west shore of the island. A count made August 1, 1956, showed a population of 1,750 sea lions on rocks surrounding Triangle Island. About 400 of these were pups.

Newcombe, Greenwood and Fraser (1918) report that prior to 1916 Triangle Island had been the location of a large rookery. The building and servicing of a lighthouse on the island from 1909 to 1920 apparently caused the colony to disband and emigrate. Some pupping was observed in 1913, but none in 1916.



FIGURE 2. Aerial photograph of rookery on rocks adjacent to Sartine Island, August 17, 1956. Taken from a Cessna 180 travelling at a speed of 80 m.p.h. and a height of 300 feet, using an 80 mm. lens on Plus-X film; 4.5 f and 1/500 sec.

Since then sea lions have repopulated these rocks and have re-established rookery colonies as shown by the 1956 observations (Table I).

Sartine Island, known locally as West Haycock, is located 6 miles northeast of Triangle Island. Few sea lions locate along the shores of the main island. Three large rocks stretch to the westward. A rookery colony is located on the middle of these (Fig. 2). This group has not previously been identified as a rookery probably because the colony is obscured from view unless closely approached. The rock formation and the distribution of the sea lions, illustrated in the aerial photograph (Fig. 2), are typical of most rookery sites in British Columbia in late summer.

Beresford Island, known locally as East Haycock, is a small rocky islet rising steeply to a rounded and wooded top about 320 feet above sea level. It is located about mid-way between Cape Scott and Triangle Island. A number of rocks lying close to the main island provide hauling-out sites for sea lions. Early in June, 1956, an estimate of 1,000 animals was made for the group. About 650, including 250 pups, were located on a large rock situated 1/4-mile northwest of the main island. This rock is known locally as "Maggot Island".

The estimate of 6,000 sea lions in the Beresford Island group in 1916 may have been exaggerated. The count was not carefully made. During the three-year interim between 1913 and 1916 more than 3,000 had been destroyed in this locality as a result of the federal bounty. From 1922 to 1938, inclusive, the Department of Fisheries accounted for the destruction of almost 5,000 sea lions, about 30% of which were pups, in this locality (Table V). In 1950, 1,861 were destroyed on the Beresford Island group. Numbers have certainly been reduced, but the group still remains one of the chief rookeries in British Columbia.

The Sea Otter Group comprises three sets of small, barren, rocky islands lying about 20 miles off the mouth of Rivers Inlet. The importance of the region for salmon fishing has been responsible for the killing of thousands of sea lions on these rocks. A federal bounty in 1914 and 1915 encouraged the destruction of sea lions in the area. Further destruction was carried out by the Department of Fisheries (Table V). From 1922 to 1937, inclusive, approximately 19,000 sea lions, about 30% of them pups, were destroyed on the Virgin and Pearl Rocks. This rate of killing averages more than 1,000 annually.

The Virgin Rocks comprise a group of three rocks lying close together about 14 miles west of Egg Island Light, and a fourth rock about a mile distant. The 1913 and 1916 censuses show 3,300 and 2,500 sea lions, respectively. The 1956 census shows only 370.

The Pearl Rocks are located 5 miles southwest of Cape Calvert. A rookery colony of 1,350 sea lions in 1913 had been reduced to 300 in 1956.

Watch Rock lies about 3 miles westward of the Pearl Rocks. In 1913 this rock accommodated a small rookery colony. Since then only an occasional non-breeding sea lion has been seen there.

The Kerouard Islands are a string of rocky islets stretching approximately 1½ miles south of Cape St. James. This group accommodates the largest single breeding colony in British Columbia. The colony is broken up into several

groups, some of which are true rookeries, while others comprise young animals, nursing cows, and apparently idle bulls. A comparison of several censuses of this colony (Table III) shows a large growth in the population since initial counts were made in 1913 and 1916.

Other sea lion locations along the coast of the Queen Charlotte Islands were surveyed by aircraft on July 17 and 18, 1957. A good count on the Kerouard Islands was not possible because of fog. Langara Rocks were occupied by 450 sea lions, and Joseph Rocks, off Tian Head, by 200 sea lions. A rock between Kootenay Point and Chads Point was occupied by 70 sea lions. A rock off Tasu Head was occupied by 55 sea lions. A rock off Reef Island was occupied by 150 sea lions. An additional 25 were seen on Marble Island, Cone Head and Cape Henry. These additions for the Queen Charlotte Islands total 950 animals. Rookery sites were found only on the Kerouard Islands.

North Danger Rocks are a group of 5 small bare rocks lying $7\frac{1}{2}$ miles south-west of Wreck Point on the west coast of Banks Island. When approached on July 18, 1956, this group was found to be occupied by a small rookery colony of 1,100 sea lions. About 300 cows with pups and 30 attendant bulls were located on one rock. Another rock was occupied exclusively by young bulls. A third rock was occupied by a heterogeneous group consisting of cows, bulls and young animals, some of which were yearlings.

Solander Island lies about one mile off Cape Cook on the west coast of Vancouver Island. When visited on May 26, 1956, a large rock located on the north side was found to be occupied by about 200 sea lions. On August 17, 1956, an aerial reconnaissance showed no sea lions on or near to Solander Island. The colony observed in May consisted of mixed sizes and sexes with no one size predominating. Some were small and judged to be yearlings, but no pups were present.

Solander Island was visited on June 17, 1916 and found to be occupied by what is described as a breeding colony of 500 animals including pups, which were large enough to take to the water (Newcombe *et al.*, 1918). These young animals were probably yearlings. On July 20, 1913, a visit to this location showed it to be deserted (Newcombe and Newcombe, 1914). Department of Fisheries counts for this locality show 200 on August 20, 1938 and 300 during the first week in August, 1955.

Other locations in which sea lions are found during the summer months are recorded in Table IV. Numbers in these locations are found to vary considerably from year to year, and at different times during the summer season. Although pupping does not occur, some breeding activities probably take place. Most of the groups are found to consist of a heterogeneous admixture of sexes and sizes. Some groups consist entirely of bulls, mostly young and probably adolescent. Other groups are dominated by large bulls and consist largely of cows and young animals, some of which are yearlings. An influx of recruits of both sexes and all ages arrives late in the summer when rookeries are disbanding.

In estimating total numbers of sea lions for the Province, some adjustments have been made to the numbers actually counted during the several

TABLE IV. Numbers of sea lions at major rookeries and hauling-out sites in British Columbia during the breeding season.

Locality	1913		1916		1938		1955		1956	
	(Biol. Bd. Can.)	(Biol. Bd. Can.)	(Biol. Bd. Can.)	(Biol. Bd. Can.)	(Dept. Fish)	(Dept. Fish)	(Dept. Fish)	(Dept. Fish)	(Fish Res. Bd.)	(Fish Res. Bd.)
Scott Islands	3,500		6,000		3,200	not observed	1,020	1,970	3,500	
Sea Otter Group	3,800		2,800		4,010		4,520	900	570	
Cape St. James and Kerouard Is.	2,000		1,000		2,000		600	4,500	4,000	
North Danger Rocks	not observed		not observed		2,000		380	550	1,100	
Solander Island and Cape Cook	none		500		200		370	200	200	
Langara Is. and West Coast Charlottes	not observed		not observed		250		350	530	not observed	
Bonilla Rocks	"		"		250		none	450	400	
Hallbut Rocks	"		"		100		none	none	none	
Isnor Rocks	"		"		200		500	250	not observed	
Butterworth Rocks	"		"		200		20	60	"	
Day Pt., White Cliff Pt., Goose Is.	"		"		500		330	260	30	
West Coast Vancouver Island south	"		"							
of Cape Cook	"		"		50		270	220	not observed	
Bright Is. and Buckle Group	"		"		none		200	200	none	
Numbers counted	9,300		10,300		13,510		8,570	10,090	9,800	
Arbitrary additions	3,000		3,000		—		3,500	1,500	1,500	
Estimated totals	12,300		13,300		13,510		12,070	11,590	11,300	

TABLE V. Sea lions destroyed in British Columbia by Department of Fisheries. Data from Annual Reports of Department of Fisheries.

Year	Location	No. of pups	No. of adults	Total no.
1922	Pearl Rocks		220	220
1923	Pearl Rocks	5	120	125
	Virgin Rocks	649	1,111	1,760
1924	Pearl Rocks	312	158	470
	Virgin Rocks	903	1,333	2,236
1925	Pearl Rocks	102	138	240
	Virgin Rocks	1,067	1,520	2,587
1926	Pearl Rocks	146	368	514
	Virgin Rocks	565	877	1,442
1927	Pearl Rocks	40	635	675
	Virgin Rocks	130	858	988
1928	Pearl Rocks	2	30	32
	Virgin Rocks	375	632	1,007
	Solander Is.		103	103
1929	Pearl Rocks	7	119	126
	Virgin Rocks	522	695	1,217
	Solander Is.			16
1930	Pearl Rocks	24	36	60
	Virgin Rocks	568	440	1,008
1931	No data			
1932	Virgin and Pearl Rocks			1,128
1933	Pearl Rocks	1	212	213
	Virgin Rocks	212	601	823
1934	Virgin and Pearl Rocks	125	663	788
1935	Virgin and Pearl Rocks	110	513	623
1936	Pearl Rocks	2	109	111
	Virgin Rocks	73	94	167
	Solander Is.		60	60
	Beresford Is.	1,043	2,476	3,519
1937	Pearl Rocks		24	24
	Virgin Rocks	95	62	157
	Solander Is.		165	165
	Beresford Is.	428	1,633	2,061
	Others		126	126
1938	Pearl Rocks	4	21	25
	Virgin Rocks	2	27	29
	Solander Is.		66	66
	Beresford Is.	256	605	861
	Sartine Is.	513	354	867
	N. Danger Rocks		122	122
	Others		760	760
1939	Pearl Rocks		13	13
	Virgin Rocks	34	105	139
	Solander Is.		141	141
	Beresford Is.	415	406	821
	Other		131	131
1940	N. Danger Rocks		75	75
	Other		59	59
1941	No data			
1942	Various localities			208
1943	" "			33
1944	No data			
1945	Virgin Rocks			42
	Other			241
1946	Various localities			304
1947	" "			282
1948	" "			113
1949	" "			358
1950	Beresford Is.			1,861
	Other			201
1951	Various localities			222
		8,730	18,976	32,755

censuses. Adjustments are shown in Table IV under the term "Arbitrary additions". An addition of 1,500 has been made to the 1956 Fisheries Research Board count on the basis of 1957 aerial counts in the vicinity of Queen Charlotte Islands, and along the eastern coast of Hecate Strait, and Department of Fisheries counts along the west coast of Vancouver Island south of Cape Cook. Careful counts were made on the Scott Islands in 1956 and the total of 3,500 is judged to be nearly correct. The censuses made by the Department of Fisheries in 1955 and 1956 have been adjusted to conform to this figure. Additions of 3,000 have been made to both the 1913 and 1916 counts to adjust for the several probable sea lion sites which were not observed during these years. Isnor Rock, located off the northern tip of Aristazabal Island, was observed from the air on July 19, 1957, and a count of 125 obtained. This figure was used to supplement counts in 1956.

Close observations and careful counts of sea lions on one concentrated rookery site, Maggot Island, provide some information which may be used as a basis for assessing the composition of the population in terms of sex, age and breeding status. In June and July, 1956, the population on this rock totalled 650, of which 250 were pups. Of 17 sexually mature cows studied, all but one were in a post-partum condition and almost every adult cow was accompanied by a pup. The size of the harems varied from 4 to 17 cows, but usually 10 prevailed at the peak of the breeding season in July. The composition of this breeding colony is approximately as follows:

<i>Class</i>	<i>Number</i>	<i>%</i>
Pups (by count)	250	38.5
Post-partum cows (one per pup)	250	38.5
Cows not post-partum (one per 17 post-partum cows)	15	2.0
Harem bulls (one per 10 cows)	25	4.0
Juveniles (estimate)	25	4.0
Others, mostly reserve bulls	85	13.0
	<u>650</u>	<u>100.0</u>

The entire population of 11,300 animals comprises 3,000 pups and 8,300 yearlings or older individuals. The sex ratio in 100 pups was found to be nearly equal. On this basis it has been assumed for the purpose of rough calculation that sexes are equal in older age groups. The total population, therefore, comprises 4,150 females, other than pups, of which 3,000 are post-partum. Of the remaining 28%, some are juvenile and some are cows nursing yearlings. The pregnancy rate for sexually mature females is, therefore, in excess of 70%.

The composition of the population is not homogeneous even within a small rookery like North Danger Rocks. Some groups where pups are found resemble the concentrated breeding colony described for Maggot Island. Other groups are composed exclusively of young bulls. Still others comprise small groups of cows, yearlings and possibly other juveniles in charge of large bulls.

The role of this latter social group in breeding activities requires further study. Direct observation has shown that some yearlings are still nursing, and that some breeding activity occurs in these groups. The available evidence suggests that some cows, probably not more than 25% in any one year, have missed post-partum impregnation and continue to nurse pups for more than a year.

Mortality factors such as disease, trampling by adults, starvation resulting from mothers failing to return or failing to find their pups after foraging expeditions at sea, drowning during early attempts at swimming, predation, and storms, confront the young of most Pinnipeds during their first few months. It is impossible to assess at this early stage of the study the extent to which each of these factors operates.

Mortality during the first 6-8 weeks of life appears to be slight in this population. Only 5 dead pups were found when the rookeries were studied in July and August. No indication of disease, such as hookworm, which accounts for a high infant mortality in fur seal (Kenyon and Scheffer, 1953), was noted. The pups all appeared to be healthy. The vulnerability of pups to storms was especially noted on certain rookeries, and no doubt catastrophic weather conditions take a toll of the young in some years. Bonnet *et al.* (1938) considered that about 25% of California sea lion pups are eliminated by accidents and drowning, and that not more than 50% of any year's crop reaches the age of one year. Evermann (1921) observed more dead pups and dying pups than live ones on the Año Nuevo rookery off California. He related this to the sea having washed over the entire rookery during a severe storm.

DISCUSSION AND SUMMARY

The populations of sea lions along the coast of British Columbia in 1956-1957 was 11,000-12,000. These are concentrated during the summer breeding season mainly in two major areas. The largest rookeries are found on the Scott Islands and the Kerouard Islands. Together, these locations accommodate between 60 and 70% of the entire population, and account for 90% of the pupping.

Some changes have occurred in the location of rookeries. Pupping no longer occurs on the Virgin and Pearl Rocks which formerly constituted a large rookery comparable in size to the Scott Islands population. The population in this area now numbers less than 1,000 as compared to 3,000-4,000 in former years. North Danger Rocks and Sartine Island are described for the first time as rookeries. Triangle Island was a large rookery prior to 1916, was subsequently abandoned as a rookery site, and has since been repopulated by rookery colonies.

Efforts to reduce the numbers of sea lions on this coast because of their reputed depredations of fish and fishing gear have resulted in the destruction of more than 30,000 animals during the past 40 years. The rate of killing has for a number of years averaged slightly more than 1,000 per year, but the population has shown no substantial reduction in numbers.

The elimination of 1,000 sea lions from a population of 12,000 is not excessive when certain factors are considered. A large proportion of those killed were

pups. Some, and possibly many, of the pups would fail to survive their first year of life. The extermination of pups which would normally have died from natural causes is superfluous. The effect of the kill in reducing the reproductive potential is more important than is its immediate effect in reducing present numbers. In this regard, it should be noted that only half the population, the cows, can potentially reproduce themselves. The killing of a few bulls will not effect the reproductive potential of a population of polygynous habits, in which there remains a reserve of male breeders. The actual annual reduction in numbers is probably much less than 1,000 and the reduction in breeding potential considerably less than would superficially appear.

The results of these control measures as they affect a restricted locality are shown by a comparison of numbers on the Virgin and Pearl Rocks with those on the Kerouard Islands. The relentless destruction of sea lions in the former locality has greatly reduced their numbers and has put a stop to pupping. On the Kerouard Islands where the population has seldom been molested, numbers have doubled in the past 40 years.

Colonies in other locations such as Bonilla, Isnor, Langara and Joseph Rocks, where pupping does not occur, show considerable annual and seasonal variations in numbers. These colonies consist of groups of mainly two kinds. One consists entirely of young bulls. Another consists of small mixed groups of cows, yearlings and possibly juveniles in charge of large bulls. Cows with nursing yearlings have been found in these groups, and such colonies no doubt contribute to breeding activities.

The 1956 estimate of 11,300 sea lions in British Columbia includes 3,000 pups. On this basis, and assuming a 50:50 sex ratio, the pregnancy rate is in excess of 70%.

The incidence of mortality during the first few weeks of life appears to be slight in this sea lion population. In consideration of evidence from other localities and the vulnerability of the pups to inclement weather, however, it is judged that storms probably cause heavy mortality among the pups in some years.

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The Estimation of Population Size by a Marking and Recapture Procedure^{1,2}

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ABSTRACT

The Schumacher and Schnabel estimates of population size are compared and reasons are given for preferring the Schumacher formula. This formula is extended to permit mortality and recruitment in the population. Confidence limits are provided according to standard regression theory.

INTRODUCTION

TWO DIFFERENT FORMULAE are available for making an estimate of population size from a marking experiment in which marking and sampling are carried out simultaneously on a closed population. One of them, derived by Miss Schnabel (1938) by the method of maximum likelihood, requires considerable arithmetic, because the equation must be solved iteratively. The other, developed by Professor Schumacher (1943) out of a weighted least squares fitting, is easier to use since it does not require an iterative procedure.

The usual practice has been, it seems, to employ the maximum likelihood estimate, using a first order approximation to avoid the cumbersome arithmetic. This note suggests that it is preferable to use the Schumacher formula, since the supposed benefits of a maximum likelihood solution cannot be guaranteed, owing to lack of randomness in the sampling. Furthermore, this formula is easily extended to allow for mortality and recruitment in the population. Estimates so formed of these parameters are subject to large errors, but at least this method is available when more powerful ones, which require the use of numbered tags, cannot be used.

FORMULAE

ASSUMPTIONS

1. The population does not change in size during the sampling. Thus mortality and recruitment must be negligible and all samples must be returned to the population.
2. All samples are taken randomly from the population.

NOTATION

N stands for the size of the population, assumed constant. Estimates of N are symbolized by \hat{N} .

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²The substance of this paper was presented at a joint meeting of the Biometric Society and the American Society of Limnology and Oceanography, at Madison, Wisconsin, 1953.

X_t represents the number of marked individuals in the population just before the t^{th} sample is taken.

n_t and x_t are the numbers of individuals and of tagged individuals in the t^{th} sample.

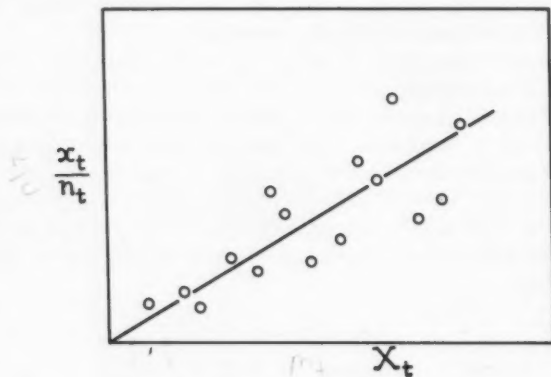
m is the number of samples.

DERIVATION OF ESTIMATES

The size of each sample will ordinarily be small compared with the size of the population and no sensible error will be committed by taking the distribution of x_t to be binomial. The mean of $\frac{x_t}{n_t}$ is then $\frac{X_t}{N}$ and the variance is

$$\frac{\frac{X_t}{N} \left(1 - \frac{X_t}{N}\right)}{n_t}.$$

We may think of making a plot of $\frac{x_t}{n_t}$ against X_t . The plotted points should, apart from the effects of error, lie on a straight line which passes through the origin and has slope $\frac{1}{N}$.



If the line is to be fitted by least squares, with each point assigned a weight w_t , the parameter $\hat{p} = \frac{1}{N}$ will be chosen to minimize the sum of squares

$$\sum_t w_t \left(\frac{x_t}{n_t} - \hat{p} X_t \right)^2.$$

The resulting equation to be solved for \hat{p} is

$$(1) \quad \hat{p} \sum_t w_t X_t^2 = \sum_t w_t \frac{x_t}{n_t} X_t.$$

THE SELECTION OF WEIGHTS

If the assignment of weights is made in the usual fashion, i.e. by choosing them proportional to the reciprocal of the variances, the values of w_i are taken to be proportional to

$$(2) \quad \frac{n_i}{\frac{X_i}{N} \left(1 - \frac{X_i}{N}\right)}$$

Of course, these values cannot be known, because they depend on N , the unknown population size. However, iterative procedures can be used to circumvent this difficulty.

Substituting weights from formula (2) into equation (1) yields the equation

$$\hat{p} \sum_i \frac{n_i X_i}{1 - \frac{X_i}{N}} = \sum_i \frac{x_i}{1 - \frac{X_i}{N}},$$

or, rearranging and writing $\hat{p} = \frac{1}{\hat{N}}$,

$$\sum_i \frac{x_i - n_i X_i / \hat{N}}{1 - X_i / \hat{N}} = 0.$$

This equation is seen to be identical with that furnished by the maximum-likelihood approach (Schnabel, 1938; DeLury 1951).

Numerical methods of solving the equation have been discussed by Schnabel, who expanded in series and truncated to yield an equation, of perhaps high degree, and by DeLury who used iterative methods.

This discussion shows that the weighting provided by the maximum-likelihood method depends on the "true" but unknown proportions of tagged individuals in the population. If the sampling is truly random, there is little doubt that these weights yield the highest efficiency in the estimation of N . In practice, however, owing to the tendency of fishes to stratify and for other reasons that lead to similar effects, the proportion of marked individuals available to the sampling at any time is likely to differ widely from the "true" proportion and the weights are therefore likely to be seriously wrong. In these circumstances, weighting by sample size alone is preferable to weighting according to proportions tagged. Hence, putting $w_i = n_i$, the estimating equation becomes

$$(3) \quad \hat{p} \sum_i n_i X_i^2 = \sum_i x_i X_i.$$

This equation is easily set up and solved. No iterations are required. Equation (3) is equivalent to the formula given by Schumacher and Eschmeyer (1943).

THE DEFINITION AND ESTIMATION OF ERROR: CONFIDENCE LIMITS FOR THE SIZE OF THE POPULATION

If the sampling is random, the whole of the error is encompassed by the binomial distributions mentioned earlier and the plotted points in Figure 1 would display only this error through their deviations from the line. Some simple approximate formulae for confidence limits, based on this definition of error, have been given by DeLury (1951).

It is to be expected, however, that deviations from biological sources, as well as the binomial sampling error, will be encountered in practice and should be included in the definition of error. The variance of this error would then be estimated from the deviations of the plotted points from the fitted line, according to standard regression theory.

If s^2 denotes the estimate of variance calculated in this way, then, for any set of weights w_t ,

$$(m-1)s^2 = \sum w_t \left(\frac{x_t}{n_t} \right)^2 - \frac{\left[\sum w_t \frac{x_t}{n_t} X_t \right]^2}{\sum w_t X_t^2}$$

and the estimated variance of \hat{p} is given by

$$s^2 / \sum w_t X_t^2.$$

100(1- α)% confidence limits for $p (= \frac{1}{N})$ are given by $\hat{p} \pm t_{\alpha s} / \sqrt{\sum w_t X_t^2}$ where t_{α} is the t -value with $m-1$ degrees of freedom corresponding to $P = \alpha$. Estimates and confidence limits for p may be converted to estimates and confidence limits for N .

EXPLICIT FORMULAE WHEN $w_t = n_t$

Weighting by sample size appears to be preferable in all respects to a more elaborate weighting which depends on proportions of marked individuals in the population. Not only are the formulae simpler but, in view of uncertainty on the score of randomness in the sampling, there can be no theoretical support for any other kind of weighting.

When $w_t = n_t$, the formulae are as follows:

$$\hat{N} = \sum n_t X_t^2 / \sum x_t X_t.$$

$$(m-1)s^2 = \sum \frac{x_t^2}{n_t} - \frac{[\sum x_t X_t]^2}{\sum n_t X_t^2}.$$

The end points of the confidence range for N are furnished by the formula

$$\frac{\sum n_t X_t^2}{\sum x_t X_t \pm t_{\alpha s} \sqrt{\sum n_t X_t^2}}$$

RELAXATION OF ASSUMPTIONS

The points plotted in the accompanying Figure may be interpreted even though mortality and recruitment may be introducing substantial effects. Let

c_t represent the number of unmarked individuals taken in the t^{th} sample, marked and released. Then the total number marked and released up to the time the t^{th} sample is taken is $T_t = c_1 + c_2 \dots + c_{t-1}$.

If a constant mortality rate μ is operating during this period, the number of marked individuals in the population just before the t^{th} sample is taken is

$$X_t = c_1(1-\mu)^{t-1} + c_2(1-\mu)^{t-2} \dots + c_{t-1}(1-\mu).$$

If, during the same period, recruitment takes place at a constant rate β , the size N_t of the population just before the t^{th} sample is drawn is

$$N_t = N_1(1-\mu)^{t-1}(1+\beta)^{t-1}.$$

The sample ratio $\frac{x_t}{n_t}$ has as its mean value the population ratio X_t/N_t , which may be written approximately, by dropping all powers of μ and β above the first and the product of μ and β ,

$$\frac{X_t}{N_t} = \frac{1}{N_1} T_t + \frac{\mu}{N_1} D_t - \frac{\beta}{N_1} R_t,$$

where

$$T_t = \sum_{i=1}^{t-1} c_i,$$

$$D_t = \sum_{i=1}^{t-1} (i-1) c_i,$$

$$R_t = (t-1) T_t.$$

Estimates of $\frac{1}{N_1}$, $\frac{\mu}{N_1}$ and $\frac{\beta}{N_1}$ may be calculated by a least squares fitting of $\frac{x_t}{n_t}$ on T_t , D_t and R_t by the standard procedures of multiple regression. Either of the second and third terms may be omitted if a fitting is required that makes allowance for mortality alone or recruitment alone.

NUMERICAL TESTS

The arguments given above for preferring the Schumacher to the Schnabel formula do not lend themselves to direct mathematical tests. Therefore the two formulae have been compared on data obtained by sampling a population of beads.

The inclusion of coefficients of mortality and recruitment in a Schumacher fitting may well fail in practice, owing to large errors in the data. To gain some insight into this question, the formulae have been tried on some data obtained by sampling a population of beads and on some lake trout data.

COMPARISON OF SCHUMACHER AND SCHNABEL FORMULAE

These comparisons are made on samples drawn from a population of 2,000 beads. Every effort was made to draw the samples randomly, so the comparisons should favour the maximum-likelihood (Schnabel) estimate. However, the two formulae perform equally well.

	<i>Estimate</i>	<i>Confidence Limits</i>	<i>Confidence Range</i>
M. L. (first approx.)	2151	1797-2631 (formula)	834
M. L. (accurate)	2136	1888-2453 (regression)	565
Schumacher	2084	1876-2344 (regression)	468
M. L. (first approx.)	1925	1732-2115 (formula)	383
M. L. (accurate)	1904	1768-2063 (regression)	295
Schumacher	1874	1755-2010 (regression)	255

COMPARISON OF MAXIMUM-LIKELIHOOD WEIGHTING AND WEIGHTING BY SAMPLE SIZE ONLY, MORTALITY INCLUDED

The sample was drawn from a population of 2,000 beans with a mortality rate of .01 per sampling interval introduced into the population.

	<i>Estimate</i>	<i>Mortality Rate</i>
M. L. weighting	2492	.0485
Weighting by sample size	2100	.0200

Weighting by sample size yields better results in this example than the maximum-likelihood weighting. This is probably accidental.

The estimated mortality rate is double the actual rate. Even so, this estimate is probably better than would be obtained in actual practice.

ESTIMATION ALLOWING FOR BOTH RECRUITMENT AND MORTALITY

These data refer to lake trout that were tagged in 1948 and recaptured in 1949 as they came to spawn. Only the records of the 1949 captures are used in the fitting, but the fact that all the individuals were tagged previously rules out the possibility of genuine recruitment.

Three fittings are carried out, weighting by sample size only. One makes no allowance for either mortality or recruitment, one allows for mortality only and the third permits both mortality and recruitment.

<i>Estimate</i>	<i>Mortality Rate</i>	<i>Recruitment Rate</i>
1349	—	—
855	-.0349	—
1023	.1686	.0962

The fitting that allows both mortality and recruitment yields high values for both. Presumably in this instance they represent emigration from and immigration to the sampling area and the results are not unreasonable. The fitting allowing mortality only fails completely to account for the data, since a negative mortality coefficient occurs. The estimate of population size when neither mortality nor recruitment are allowed for is judged to be not unreasonable.

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The Rôle of Competition in the Mortality of Hatchery Trout¹

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ABSTRACT

The literature on the survival of hatchery-reared trout after release in streams is reviewed and the conclusion is reached that survival is poor in lakes and streams where a resident trout population already exists. In streams the deaths of planted trout occur very soon after their release and have been referred to as "delayed mortality". However, a comparison of survivals after planting in occupied and non-occupied streams shows that many of the deaths are not attributable to hatchery-background or transportation methods, but largely to some aspect of competition with resident trout. Some investigations which have sought to measure the relative survivability of wild and hatchery trout have not used *resident* wild trout and thus a crucial aspect of the competition has been omitted. Investigations at the Alberta Biological Station test stream, Gorge Creek, are described; in these a significant difference in blood lactic acid levels was found between hatchery trout with and without competition from resident trout. A tentative role is assigned competition as follows: introduced trout must compete for niches and for food. In the early stages of this competition they are continuously exercising; they exhaust stores of some metabolite and die either of acidosis or starvation.

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I. INTRODUCTION

A PROBLEM of major importance to fishery managers is the high mortality that occurs among hatchery-reared trout after they have been released in a stream or lake. It is the purpose of this paper to present the evidence that has been gathered concerning this mortality, to review briefly the investigations and

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speculations concerning its cause, and to offer a concept of the manner in which competition may play a major rôle.

At the present time the theory that competition may be important in the survival of hatchery fish is somewhat in disrepute among fishery biologists. This is partly, if not entirely, due to a failure to appreciate precisely what is implied by the term "competition". An excellent example of this lack of understanding is provided by an anonymous footnote on page 14 of the *Progressive Fish-Culturist*, No. 18, 1956, which cites a starvation experiment on rainbow and brown trout. Many of the trout were able to survive 248 days without food. From this fact the footnote concludes that it is doubtful if competition between wild and hatchery trout is important. Evidently, the author of the footnote thinks of competition as being competition for food. Much of the recent and current work on survival of hatchery trout in the presence of wild trout has been planned with the obvious, but not explicit, assumption that competition is solely *competition for food*. Before proceeding to the main purpose of this paper, therefore, it seems worthwhile to examine the concepts of competition that have been expressed by its serious students.

Charles Darwin (1859) first emphasized the importance of competition when he explained the part it played in natural selection. Darwin's idea of competition was the demand of more than one organism for the same resource of the environment in excess of immediate supply. It is quite clear that "resource" includes food supply but is not restricted to it. Implicit in Darwin's concept of competition is the factor of elimination. Any two species could not indefinitely occupy *identical* niches—one would disappear. Support for the "elimination" hypothesis was provided by Elton (1946). In a survey of the literature on ecological communities he pointed out that 85 per cent or more of the species in any one community are sole representatives of their genera; apparently interspecific competition had eliminated all but one species of each genus in each ecological community. Crombie (1947) reached similar conclusions, and in a survey of the literature on interspecific competition, concludes that Darwin's original thesis is adequately supported by facts from both field and laboratory.

Park (1954), reporting on his beautifully designed laboratory studies of competition between two beetle species, suggested interspecific competition to be . . . "those new events that emerge when two species populations coassociate and which lead in time to the persistence of one species and the selective elimination of the other". In Dr. Park's experiments two species of flour beetle were cultured together in vials of flour under a variety of conditions. In every case, one or the other species was eliminated. The definition amounts to expressing what competition is in terms of its result. What was implicit in Darwin's concept becomes explicit in Park's, and *vice versa*. Since it is not established by what mechanism competition caused one species of beetle to die out, the concept of demand for some resource in excess of supply is omitted from the definition.

For the student of competition in the field, Dr. Park's definition is not satisfactory. Field studies may demonstrate that some kind of interaction between two species is producing measurable effects on one or both species, but

that these effects are not necessarily mortal. A good example is the careful study by Larkin and Smith (1954) on the effects on Kamloops trout produced by the invasion of their habitat by reddsided shiners. The shiners depressed the growth rate of the trout by a full year. This result appears to have been achieved by competition for bottom organisms and by mutual predation, the shiners on trout fry and the adult trout on shiners. In a recent review of competition in freshwater fishes, Larkin (1956) accepts the Darwinian definition.

To Darwin's definition of demand in excess of supply, Solomon (1949) added two more points: (1) direct, active struggle between individuals or groups; and (2), the occupation or consumption by earlier arriving individual of something in limited supply, so that late-comers are automatically excluded or deprived. It may be argued that these two points are really contained in Darwin's broader statement; however, both points are useful in directing attention toward the mechanism by which competition may operate. They are particularly pertinent in the study of competition between wild and hatchery-reared trout, which, as will be argued, seems to consist of competition for *Lebensraum* that involves both active inter-individual struggle and struggle against environmental forces.

The nature of the data to be discussed is such that it is not profitable to distinguish between interspecific and intraspecific competition; the situations created by stocking hatchery trout are much the same whether the species stocked is the same or not the same as the wild resident species. In this paper, competition is used in the Darwinian sense as applied to mutual interactions between two species.

II. DIFFERENTIAL SURVIVAL OF HATCHERY-REARED AND WILD TROUT

In the past twenty years a great deal of effort has been expended in measuring the catches of hatchery-reared trout after planting in streams and lakes. This work has been thoroughly reviewed by several authors (Miller, 1949; Smith, 1948; Schuck, 1948); since these reviews appeared, recent papers by Mullan (1955), Burdick and Cooper (1956) and Hale and Smith (1955) have provided further evidence. Broadly, it has been found that trout fry planted in lakes or streams containing breeding resident trout populations are taken in insignificant numbers by anglers. Such plantings have been largely abandoned. Instead, much larger trout were planted, at first in the fall. Again, returns were too low to justify the costs of the operations. The best returns (in lakes and streams with breeding residents) were obtained from legal-sized trout planted immediately prior to and during the angling season. The success of these plants varied somewhat from place to place, but a reasonable average return would be about 35% of the numbers planted. Detailed creel censuses in streams revealed that three-quarters of the returns were made in the first week or two after the release of the trout. Negligible numbers were creeled in the second summer, i.e., few or no planted trout seemed to have survived their first winter. Returns from lakes have been better, particularly in lakes where no resident population existed prior to planting. However, it has been frequently observed that these

lakes do not continue to provide good fishing but deteriorate markedly in three to five years.

The studies referred to in the preceding paragraph do not, of course, demonstrate any differential mortality. In fact, the failure to catch more than, say, 35% of a planting does not necessarily mean that the other 65% died. However, the inference is strong that most of the uncaught fish did die; and if they did, the mortality rate exceeds that observed for wild trout. The studies of Nielsen *et al.* (1957) and of Miller (1952, 1954b, 1955) provide less inferential evidence. The former authors released trout in screened-off sections of Convict Creek. These sections could be deprived of their water, the pools pumped dry, and the fish recovered and counted. This work will be discussed in detail in a later section. For the present, let us examine Miller's experiments.

THE GORGE CREEK EXPERIMENTS

Gorge Creek is one of the test streams of the Alberta Biological Station. It is located on the Eastern Slopes of the Rocky Mountains in Alberta, at an elevation, at its mouth, of 4,800 feet (1,460 m.). The stream and the experimental design have been previously described (Miller, *opera citata*). Briefly, Gorge Creek is a small, tributary stream, 6 miles (10 km.) long and 15 to 30 feet (4.5-9 m.) wide, flowing through steep shale banks into the Sheep River. It forms a series of gentle runs and rocky pools providing homes for about 1,000 small adult cutthroat trout per mile. There are no other fish species. Fish-proof sections were formed by building removable wood and wire fences across the stream at intervals of $\frac{3}{4}$ -mile. Into one or more such sections, tagged, individually weighed, hatchery-reared cutthroat were released. Daily patrols of the sections were made, dead fish weighed and recorded, and living fish caught, weighed and released.

The results of many of these experiments have been reported in the papers already cited. When planted in sections containing resident trout, $\frac{1}{3}$ of 3-year-old hatchery fish and 50% to 60% of 2-year-old hatchery fish died during the first two weeks of the experiment. The experiments usually lasted from June through September. During this time few or no wild trout died. Thus, there was demonstrated a very pronounced differential survival.

III. CAUSES OF DIFFERENTIAL SURVIVAL

The greater mortalities of hatchery-reared trout have been generally ascribed to some failure in the hatchery technique. Schuck (1948) reviewed the literature dealing with returns of planted trout to anglers, concluded that these returns were too low, and suggested a number of features of the hatchery background that might account for the situation. Schuck's list included food, constant water temperatures and various water conditions. Some support for these ideas is provided by experiments in which survival of trout from different hatcheries exposed to similar conditions is compared. It was found that certain hatcheries produced a more viable trout (see Nielsen *et al.*, 1957).

Wales (1954) and Miller (1954b) both suggested that the absence of natural selection in the hatchery could account for the poor showing in the streams. Under natural conditions only about 1% of the fingerlings produced in the stream will survive. In the hatchery 40% or more are normally reared to legal-sized trout for planting.

The rôle of competition in differential survival has received considerable attention. Field experiments have been conducted by Miller (1955, and others to be described in this paper), Adelman and Bingham (1955) and Nielsen *et al.* (1957). The work of Black (1955, 1956, 1957) on the rise of blood lactate in exercised trout has an important bearing on the competition problem, particularly as his results suggest a possible mechanism by which competition could act.

In this section a series of experiments which have a bearing on the differential survival problem will be reviewed and some previously unpublished work will be described. The material has been grouped under two headings: Rôle of natural selection; and Effects of resident populations.

RÔLE OF NATURAL SELECTION

As previously mentioned, the small degree of natural selection in the hatchery has been suggested as a cause of the lower survival of hatchery trout. Fish reared in the quiet waters of a pond and fed regularly have been subjected to very little environmental pressure. When such fish are placed in a stream they are immediately exposed to much harsher conditions; perhaps those that would have died as fry or fingerlings, had they hatched in the stream, now succumb to environmental forces. A series of experiments done at Gorge Creek serve to substantiate this supposition. Portions of this work have been published (Miller, 1955); for the sake of completeness these portions and the unpublished data will be presented here together.

When it was established by several summers' experiments that 50% to 60% of the hatchery 2-year-olds died after release in a populated enclosure of Gorge Creek, the next step was to determine the survival of two other groups: these were first, wild fish, taken from Gorge Creek above the experimental enclosures and transferred to an enclosure; and second, trout which had been hatched in the hatchery but reared under natural stream conditions.

SURVIVAL OF WILD CUTTHROAT TROUT. In a first experiment, 152 trout were caught by angling in the upper portions of Gorge Creek; these were given numbered Petersen-type tags, weighed and carried in pails of water to an enclosure lower down the creek. Here they were released to find a living in competition with approximately three hundred resident wild trout. Only 2.4% of these trout succumbed to natural causes during the summer (Some were killed attempting to get through the upper screen of the enclosure; these have been considered "unnatural" mortalities.) The weight record is interesting: during their first 30 days in the enclosure the transplanted trout lost weight; the lowest average value was reached on the tenth day, when they weighed 90.5% of weight at transfer. By the fortieth day the fish had regained all lost weight and, from then on, made small gains.

A similar experiment was performed two years later (1953). In this, 209 wild trout were caught outside the enclosure area, tagged, weighed and transferred to the enclosure. During the summer 4.3% died. A maximum weight loss of 14.7% was observed; this was regained after 50 days.

Recoveries of fish from the first experiment were made in the two years following transfer and showed that 46% survived the first winter and 29% the second winter; these are the usual survival percentages for wild trout in Gorge Creek.

SURVIVAL OF STREAM-REARED HATCHERY TROUT. Two experiments have been carried out using trout which were hatched in the hatchery and then transferred to Bighill Creek. Bighill Creek contained no resident trout but offered typical trout stream habitat. The hatchery fish were retained by screens and left to fend for themselves, i.e., unfed.

In the first experiment several hundred trout that had spent one summer in the hatchery rearing pond were transferred to Bighill Creek and left there for 18 months. Then 58 of them were moved to an enclosure in Gorge Creek. Shortly afterward a flood washed out the screens and an unknown number of fish escaped. However, 27 were recovered by angling the same summer and 10 in the next summer. Thus at least 17.2% survived the winter. Weight records show that these trout lost 8.8% of their weight in 40 days, and that this was regained by 50 days.

A second experiment in 1954 used trout that had spent one summer in a rearing pond and 10 months in Bighill Creek. Seventy-six were transferred to an enclosure in Gorge Creek where 18.4% died during the summer. These fish lost 11.7% of their weight in 10 days but thereafter rapidly regained and were in excess of planted weight by the twentieth day.

These experiments demonstrate that under similar stream conditions, and in competition with a resident population, three grades of survival exist. The best survival of more than 90% is shown by transplanted wild trout; a middle grade of approximately 80% is shown by fish exposed to natural selection in a stream before planting; and the poorest survival is exhibited by pond-reared fish—40 to 50%. These findings certainly suggest that the low degree of natural selection in the hatchery may account for at least some of the poor survival of hatchery trout.

EFFECTS OF RESIDENT POPULATIONS

The experiments reported above were all carried out by superimposing the experimental fish on a resident population. A number of experiments have been reported in which an effort has been made to assess the effects of these resident trout on the survival of the introduced trout.

THE GORGE CREEK EXPERIMENTS. The first experiment at Gorge Creek designed to test the effects of the resident trout on the survival of the hatchery trout was done in 1954 and has been reported (Miller, 1955). In this study two similar sections were screened off; in one, all the resident trout were killed with a rotenone poison; in the other the resident population of 340 catchable-size

trout was left undisturbed. Into each section approximately 200 tagged, weighed, hatchery cutthroat trout were released. Two such releases were made in the no-competition enclosure.

A similar experiment, using the same two enclosures, was done in 1955 (unpublished) using brown trout and brook trout. The results of the two years' experiments are summarized in Table I.

TABLE I. Mortality and weight changes during the summer of release of brook, brown and cutthroat trout with and without competition from resident cutthroat trout. CT = cutthroat trout; BT = brown trout; EB = brook trout.

	No Competition			Competition		
	1954		1955	1954	1955	
	Lot I CT	Lot II CT	CT	CT	BT	EB
Mortality (%)	16.0	12.4	10.5	54.5	59.2	49.5
Percentage of planted wt. after 50 days	127.3	110.5	218.0	98.2	93.0	100.0
Av. wt. at planting (ounces)	1.03	1.6	1.4	1.5	5.4	2.2
Wt. range (ounces)	0.5-3.0	1-4.5	1-3.5	0.5-5.0	1-11	1-4.75
No. planted	200	121	200	200	86	113

The mortality figures in Table I were obtained by actual counts of dead fish. The two stream sections were patrolled at least once each day, usually twice; the dead fish were picked out of the water, weighed and their tag numbers recorded. During the two summers no resident trout were found dead. The mortalities recorded in this way represent minimal values; dead fish not found or fish taken by predators are not included. However, predators are very rare in the area, and their effect is probably negligible; also, in the clear water, dead fish are very conspicuous and not likely to be overlooked. It is believed that the mortality figures are very close to the true values. Table I shows remarkably consistent results: hatchery trout in competition with resident wild trout suffered a mortality of 49.5-59.2%. Differences between mortality of brook, brown and cutthroat trout lie within the probable experimental error, although the brook trout appear to be slightly more resistant. The resident trout with which the hatchery fish were in competition ranged from 1 to 5 ounces (30-140 g.) in weight, average 2.6 ounces (74 g.); they had, then, no advantage in size over the brown trout, and only a slight advantage over the other two species.

All the competing species lost weight; after 50 days the survivors had completely (brook) or nearly (other species) regained their weights at planting time.

In sharp contrast, the hatchery trout planted in the enclosure from which the resident trout had been removed, suffered mortalities of only 10.5 to 16.0%. This is approximately one-quarter of the mortality of the fish faced with competition. It is well to remember that these fish (competition and no-competition groups) were in the same stream at the same time, separated only by a wire fence.

The weight changes in the two groups also show a sharp difference. The trout without competition show substantial increases; the average weight of those of one group more than doubled in 50 days. The detailed field records show that the weight gain began as soon as the fish were released in the experimental enclosure.

Survival over the first winter cannot be absolutely determined in Gorge Creek. The screens forming the enclosures are removed in the late fall and the fish are free to move down into the Sheep River. A few recoveries in the Sheep River have been made by angling; thus it is known that some do move down. It is believed the majority remain in the same enclosure area, where they are recovered by seining or rotenone poisoning the next spring. Figures obtained in this way indicate over-winter survivals of 15 to 18% for hatchery trout without competition and 3.5 to 13.3% for trout with competition (though, of course, once the screens are removed, both groups are exposed to competition).

These figures on over-winter survival, because of the unknown degree of emigration, are not believed to be reliable. Weights obtained in the second summer, however, are not subject to error and indicate significant differences. Weights of fish that had one summer without competition range from 137 to 226% of planted weight; weights of fish that had continuous competition range from 60 to 147% of planted weight.

DATA FROM OTHER STREAMS. Mullan (1956a) has found that, in Massachusetts streams, the anglers catch a higher percentage of the larger than of the smaller stocked trout. This was true of brook, brown and rainbow hatchery trout. This implies that the larger trout survived in greater numbers, presumably because their size helped them in competition with the resident trout in the streams. The same author (Mullan, 1956b) has conducted some preliminary work on stream reclamation with fish toxicants. He finds evidence of better survival of stocked rainbow and brook trout after the resident population has been eliminated or thinned out, thus eliminating or reducing competition.

DATA FROM LAKES. The technique of sport fish management made a great advance with the discovery of lake reclamation. Reclamation is the fundamentally simple process of applying fish toxicant to lakes and killing all, or nearly all, the resident fish population. After the water has lost its toxicity, trout are planted, usually as fry or fingerlings. The growth and survival of trout in these reclaimed lakes has been spectacular, and the technique has become a well-established management practice in several western states. In the past few years this type of management has spread to the mid-west and, in experimental stages, to the eastern states.

A generally admitted drawback to this management technique is that only the first stocking of hatchery trout exhibits the remarkable growth and survival. Each year after the first stocking the growth and survival of the current year's stocking grows poorer; after four or five years, survival may be negligible. So far, this history of poorer growth has been sparsely reported. Curtis (1951) has described one California lake in which a great improvement in yield from fingerling plants followed the removal of a resident population of four species of

salmonids. Burdick and Cooper (1956) have published the history of plantings of fingerling rainbow trout in Weber Lake, Wisconsin. They bring out one point pertinent to this discussion: the survival in terms of returns to anglers was markedly reduced following the good survival of a previous year's planting. Thus 10,000 two-inch rainbow fingerlings planted in 1951 yielded only five fish; at this time survival of the 1950 planting of 10,000 three-inch rainbows was good. Miller and Thomas (1957) found that in one Alberta lake that contained no resident fish, the rainbow trout reached 13 ounces (37 g.) during the summer in which they were planted; a similar plant in the following year reached only 10 ounces (28 g.) in the same time; and in the third year, a weight of only 5 ounces (14 g.) was achieved.

All of this suggests that a resident population in lakes has the same competitive advantage over introduced fish as it has in streams. The magnitude of the effect is not precisely known and it is difficult to design an experiment in a lake that would yield precise or absolute mortality figures.

IV. THE RÔLE OF COMPETITION

In the preceding section it has been shown that hatchery trout suffer much heavier mortalities in the presence of a resident wild population. The mechanism by which the resident trout exert their deleterious effects on the hatchery fish has been largely a matter of speculation. Preoccupation with the idea that competition for food is the major factor has influenced the design of a number of experiments.

COMPETITION FOR FOOD

The importance of competition for food in fresh water fish populations has been recognized for a long time. Intraspecific competition is believed to be the cause of stunting in crowded populations and there are many examples of increased growth rates in fishes following reductions in their numbers by winter kills, or by heavy exploitation. The technique of fish pond management is based to a large extent on the need of preventing overpopulation with resultant stunting. The demonstration of reduced growth rate in Kamloops trout caused by competition for food with shiners has already been mentioned (Larkin and Smith, 1954).

The feeling that competition for food is unimportant in the survival of hatchery trout has its origin in the short time it takes for hatchery trout to die after their release. Reimers (1957) has shown that trout can live through long periods without food. Trout kept at low temperatures in outside ponds suffered 17.7% mortality after 120 days of starvation; at the same temperature in indoor ponds the mortality was 9.3%. In another experiment lasting through 180 winter days, only 2.0% of starved hatchery rainbow trout died and 8.0% of wild brown trout.

Adelman and Bingham (1955) planted wild and hatchery-reared brook trout together in screened-off enclosures of two Michigan streams. In Hunt

Creek 102 wild brook trout *from another stream* and 100 hatchery trout were used; after six months 28% of the hatchery and 59% of the wild fish were still alive. In a footnote the authors state that other fish (resident?) were in the experimental section so that it carried six times its normal population. In Slagle Creek 35 trout from Slagle and 90 hatchery trout were enclosed; after six months 64% of the hatchery and 37% of the wild trout were alive. Slagle Creek, during the experiment, carried three times the normal population. The authors conclude that there is no difference in viability of wild and hatchery-reared brook trout. However, this conclusion is rendered somewhat dubious by the unusual situations which prevailed in the experimental enclosures, and the inconsistency of the results. The trout used in the experiments were not only competing with each other, but also with a large population of other trout, possibly resident. Of greater value would be the differential survival figures for the fish already in the enclosures and the fish added, both wild and hatchery-reared.

An intensive six-year study of the survival of hatchery-reared rainbow trout was carried out in sections of Convict Creek, California, by Nielsen *et al.* (1957). The authors used four equivalent sections of the stream, separated by screens, and so laid out that the water could be diverted and the sections rendered dry for a complete and accurate count of fish. At the beginning of an experiment *all* trout were removed; then hatchery-reared, catchable-size rainbow trout were stocked with wild brown trout in one section, alone in another, and wild brown trout alone in a third section. All the wild trout were secured by seining in other parts of the stream, i.e., they were *not resident trout*. In none of the experiments was an initial high mortality observed; there were no significant differences in survival in the different sections. Survivals over summer periods varied from 36.8 to 85.1%.

The results of these experiments led the authors to believe that there was no difference in survivability of hatchery-reared and wild trout. However, as in Adelman and Bingham's work, the experimental design was such that important aspects of competition were not measured. Both hatchery and wild stocks were released simultaneously into a strange locality. The effect of a *resident* population was missing and it is not surprising that the heavy mortalities which normally follow plants in *populated* waters did not occur. It is pertinent to note that in 1953, section 2 of Convict Creek contained a rainbow trout population left over from the previous year. The rainbow superimposed on this resident group showed the lowest survival of that year's lots—39.8% as compared to 48.1, 76.6 and 76.1% in Sections 1, 3 and 4 (Nielson *et al.*, Table 15). The whole investigation shows that, *under the conditions established by the experiment*, hatchery-reared rainbow trout and wild brown trout are evenly matched.

DELAYED MORTALITY AND BLOOD LACTATE LEVELS

For some years it has been well known that the mortality following planting of hatchery trout occurred mainly during the first week. Recently Horton (1956) has described this initial mortality as it has been observed in Oregon waters. In Oregon it has been known as "delayed mortality". Horton writes that it

begins 24 hours after release of the trout and reaches a peak on the third or fourth day. The average total mortality is 10% but it may reach 93% in any one planting. The mortality begins with apparent nervousness in the fish; they school and swim in circles, rising often to bite at the surface; later the fish act as if they were blind and had lost their equilibrium. They jump out of the water or plunge into the bottom. Following this stage, some of the fish die, mouth agape.

Horton conducted a series of experiments in a search for methods of reducing the mortality. He loaded a hatchery truck, took the fish on a six-hour run and returned to the hatchery of origin where the fish *were placed in ponds, by themselves*, for seven-day observation. The runs were made at different water temperatures, using different aerating systems and varied methods of loading and unloading. Anaesthesia with sodium amytol was also tried. Significant differences in delayed mortality were associated with temperature and aeration methods.

In these experiments Horton actually tested the effects of various transportation methods on subsequent survival. Since the trout were returned to ponds in which they were not faced with competition, true "delayed mortality" was excluded from the tests.

Black (1955) measured the lactic acid concentration in the blood of various fishes in an unexercised state and again after 15 minutes of vigorous exercise, induced by chasing the fish in troughs. He found that in Kamloops trout yearlings blood lactate varied from 14.7 to 17.1 mg. %, unexercised, and from 99.5 to 100.2 mg. % after exercise. In Kamloops trout 2-year-olds the corresponding figures were 8.0 and 82.2 mg. %.

J. H. Wales pointed out to Dr. Black the phenomenon of "delayed mortality"; Black suspected that the prolonged exercise associated with transportation to the planting site might increase blood lactate levels to the point where lactic acid was a significant factor in the mortality. Accordingly (Black, 1956) he carried out an experiment in which hatchery trout were given a 90 minute trip in a tank truck and returned to the hatchery troughs. In two-year-old Kamloops trout the blood lactate was 51.0 mg. % during the first four minutes after the trip was completed. The lactate remained at this level for 20 to 24 minutes, then declined erratically to resting levels after two hours. Similar trout after 15 minutes exercise showed blood lactate levels of 75.7 mg. %; lactate rose for two hours after exercise to a peak of 117.0 mg. %, then declined to 20.4 mg. % after eight hours. Black got essentially similar results with 1.5-year-old lake trout after runs in the hatchery truck, except that blood lactate increased for one hour following the trip, then declined to resting levels after two hours.

These experiments suggest that rise in blood lactate *during transportation* cannot be responsible for delayed mortality. This is not surprising in view of the author's findings, described earlier, in which delayed mortality did not occur in trout planted in a stretch of Gorge Creek from which the resident trout had been removed, but did occur in the same hatchery stock, planted in another

section of Gorge Creek in which the native trout were still present. The possibility that the resident native trout create a situation which leads to continued high blood lactate levels in the introduced hatchery fish seemed worthy of investigation. Such an experiment was done at Gorge Creek in 1956.

BLOOD LACTATE EXPERIMENTS AT GORGE CREEK

The same two sections of Gorge Creek that were used in earlier survival tests were used in the present experiments. Section I consisted of $\frac{3}{4}$ -mile (1.2 km.) of Gorge Creek, screened at each end, from which all resident trout were removed by application of a rotenone poison. Section II, above section I, was the same length, but contained a resident population of approximately 300 native cutthroat trout which weighed from 0.75–5.75 ounces, average, 2.6 ounces (21–163 g., av. 74 g.). These sections will be called No-competition Enclosure and Competition Enclosure, respectively.

On July 13, 1956, 204 tagged hatchery-reared cutthroat trout, ranging from 1.5 to 5.75 ounces in weight, average 2.6 ounces (42–163 g., av. 74 g.) were released in the Competition Enclosure. Blood samples were taken from some of them just before they were poured into the stream. The technique used was that of Black, and we are greatly indebted to Dr. Black for detailed advice given in personal correspondence.

The fish were planted in the morning; that afternoon a flash flood followed a severe rain storm; the lower screens of the Competition Enclosure were washed out and an unknown number of the trout was lost. However, 73 were later recaptured in the Enclosure, enough to carry on with the experiment.

On July 25, 1956, 12 days later, 181 tagged hatchery cutthroat trout weighing from 0.5 to 3.0 ounces, average 1.5 ounces (14–85 g., av. 42 g.) were released in the No-competition Enclosure. Blood samples from several were taken immediately before release. The later planting date was chosen to help eliminate variables introduced by fluctuating stream conditions; if the two plantings had been made on the same date observed changes in blood lactate, following planting, might be due to identical stream flow rates which would obscure any effects of presence or absence of resident trout.

In the 60 days following the plantings, blood samples were taken at more or less regular intervals from 60 fish in the Competition Enclosure and 43 fish in the No-competition Enclosure. In addition blood samples were taken from 12 wild trout in the Competition Enclosure. The fish were caught by seining and the blood samples taken immediately on the stream bank. At the same time the fish were weighed and a daily record of mortalities was kept.

An interesting observation during the early weeks of the experiment was that the Competition Enclosure fish appeared to be exhausted; they could be caught in many cases by simply bending over and picking them up in the hand. Conversely, the No-competition trout were, at all times, as difficult to catch as the wild trout.

The total mortality of fish in the No-competition Enclosure was 9.4% a figure in good agreement with previous findings of 10.5, 12.4 and 16.0% (Table I). Only 34 fish (16.7%) were found dead in the Competition Enclosure;

this figure has little meaning because of the loss of an unknown number when the screens washed out.

TABLE II. Weight changes in hatchery-reared cutthroat trout after release in enclosures in Gorge Creek.

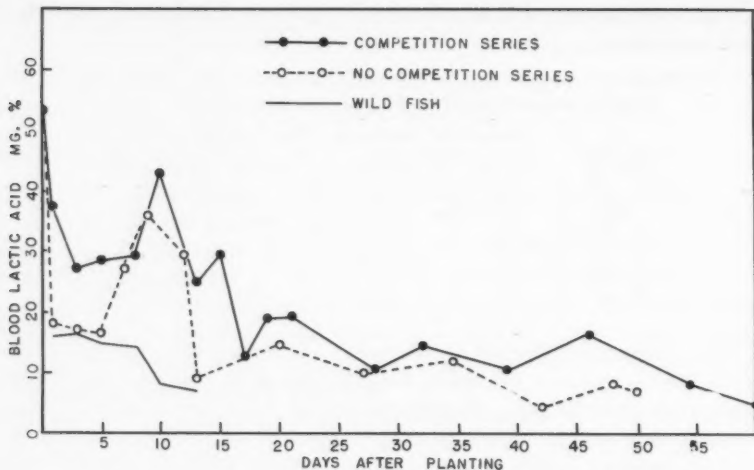
Days after planting	Competition Enclosure		No-Competition Enclosure	
	No. fish	% planted wt.	No. fish	% planted wt.
0-10	19	91	15	99
11-20	24	101	23	104
21-30	9	96	3	100
31-40	7	87.5	11	106
41-50	9	92	7	112
51-60	5	84.5	0	—

The Competition Enclosure fish were, on the average, an ounce heavier than the No-competition Enclosure trout at the start. Despite this advantage, the data show that they consistently lost weight during the summer (Table II). Conversely, the smaller trout in the No-competition Enclosure exhibited a general increase in weight. These results serve to confirm previous findings reported earlier.

The results of the analysis of the blood lactic acid are shown in Table III. The analyses were performed using the Barker-Summerson technique, also employed by Dr. Black. We wish to acknowledge our considerable indebtedness to Dr. H. B. Collier, who undertook most of the work in the analyses.

TABLE III. Blood lactic acid (mg.%) in hatchery-reared cutthroat trout with and without competition from resident wild trout.

Days after planting	Competition			No Competition		
	No. of samples	Mean lactic acid	σ_M	No. of samples	Mean lactic acid	σ_M
0	—	—	—	5	53.1	± 27.3
1	8	37.3	± 5.1	4	19.3	± 11.7
3	4	27.1	± 6.9	3	16.9	± 3.7
5	4	28.5	± 10.1	2	16.5	± 7.5
7	—	—	—	3	27.1	± 11.4
8	4	29.4	± 12.7	—	—	—
9	—	—	—	3	36.0	± 7.0
10	4	42.9	± 10.2	—	—	—
12	—	—	—	3	29.5	± 9.5
13	6	24.8	± 5.2	2	8.9	± 0.5
15	2	29.6	± 2.6	—	—	—
17	4	12.6	± 4.2	—	—	—
19	3	19.1	± 5.7	—	—	—
20	—	—	—	3	14.7	± 10.7
21	3	19.5	± 3.9	—	—	—
27	—	—	—	3	9.9	± 0.05
28	3	10.7	± 0.4	—	—	—
32	3	14.7	± 4.7	—	—	—
34/5	—	—	—	3	12.1	± 5.0
39	3	10.7	± 5.4	—	—	—
42	—	—	—	3	4.5	± 1.8
46	3	16.5	± 5.4	—	—	—
48	—	—	—	3	8.3	± 1.5
50	—	—	—	3	6.9	± 3.5
54/5	3	8.2	± 2.7	—	—	—
60	3	4.7	± 4.2	—	—	—



Lactic acid content of trout blood after release in Gorge Creek.

The data in Table III have been used to prepare the accompanying Figure, which shows the changes in blood lactic acid plotted against time. The highest lactic acid levels were found immediately after the 60-mile trip by non-aerated tank truck from the hatchery. After planting, both groups of trout showed a decline in blood lactate, followed by a rise on the ninth and tenth days. Thereafter, the levels fell gradually to the resting levels found by Black (1955) in two-year-old Kamloops trout of comparable size.

Also shown in the Figure are the 12 samples from wild trout in the Competition Enclosure. They are plotted on the same time scale as the Competition hatchery trout, i.e., zero time is July 13. The blood lactate level began at 16.0 mg. % and declined to 6.5 mg. % by day 13. This change could represent either the effects of decreasing rates of stream flow (after the flash flood on July 13) or a response, followed by adjustment, to the introduced hatchery trout. An experiment is being planned to investigate these alternative explanations.

A number of reasonably firm conclusions may be drawn from the results of this experiment:

(1) During the first 15 days there is a large difference (roughly 8 to 16 mg. %) in the blood lactic acid of the two groups of trout. The Competition group is higher.

(2) In this same period the lactic acid level in the Competition group is approximately three to five times the normal or wild level. In the No-competition group it varies from two to four times the wild level.

(3) The initial drop in both groups, followed by rises on the ninth and tenth days, is a real phenomenon, not associated with water conditions. This is known because zero time was July 13 in one group and July 25 in the other. This phenomenon suggests that some metabolite is very soon exhausted and that a period

of four or five days passes before the stock is replenished. This fits well with the observation that the trout begin feeding normally three or four days after release.

(4) The observed post-planting mortalities correspond in time with the observed period of high lactic acid levels. Table IV shows a summary of mortalities of various plantings of hatchery fish in sections of Gorge Creek occupied by wild trout.

TABLE IV. Post-planting mortality in four groups of 2-year-old hatchery-reared cutthroat trout superimposed on resident populations in Gorge Creek.

Days after planting	1950 200 trout	1952 200 trout	1954 200 trout	1955 199 trout
0	0	7	0	0
1	0	62	13	1
2	1	9	4	5
3	3	24	3	4
4	12	0	6	6
5	16	0	4	5
6	22	2	8	3
7	14	2	4	7
8	10	2	7	4
9	5	1	19	3
10	4	3	10	5
11	2	0	6	3
12	3	2	0	6
13	0	0	6	2
14	2	1	3	4
1-14	94	117	93	58
Total for summer	112	132	109	107
Percentage within 14 days	84	89	85	54

It is clear from Table IV that most of the trout die during the two weeks after planting—the period of high lactic acid levels. The lesser mortality of the 1955 plant may be because these trout were reared in circular wooden tanks with vigorously circulating water that kept them constantly swimming; all the others were reared in conventional rectangular ponds.

V. DISCUSSION

It is a firmly established fact that hatchery-reared trout, when superimposed on a resident population, suffer very heavy mortalities; in streams a number of convincing investigations have demonstrated that the bulk of this mortality occurs in the first two weeks following plantings. The events in lakes are less well-documented but there is ample evidence that survival is poor when a resident population is present. It is also firmly established that survival is very good when there are no fish resident in the lake or stream into which the hatchery trout are released.

Experiments made to determine the cause of this so-called "delayed

mortality" have failed to take proper account of the effects of the resident population. The effects of various feeding regimens in the hatchery, water temperatures, handling methods and transportation methods have been studied *but not in fish subjected to competition*. The experimental animals have been returned to hatchery ponds for observation. Thus these investigations measure only the portion of the mortality which may be due to events which take place before the trout are released in the stream or lake.

Other investigators have recognized that competition with wild trout may be a factor in mortality. However, there has been a general failure to recognize the importance of the wild trout being *resident*. Extensive studies have been conducted on the relative survival of wild and hatchery-reared trout in the same stream but, in every experiment, the wild fish were introduced to the study section *from some other place*; i.e., they were not residents. It is perhaps not surprising that no significant differential mortalities were observed under these conditions. Complementary studies established that trout could tolerate long periods of starvation. These two observations were interpreted, quite unjustifiably, as indicating that competition for food was not a factor in survival of hatchery trout.

There are a number of ways in which competition may exert effects that are not directly concerned with food supply. We are just beginning to learn something of the complexities of territorial behaviour and aggressiveness in fishes. Gerking (1953), Allen (1951) and Miller (1954a) have provided evidence that stream fishes have definite, rather limited territories that they inhabit throughout life. Newman (1956) has shown that these territories are defended; approaches of other fish of the same or different species are repelled. In fact a social order resembling the classic peck order in chickens exists in a population of stream trout.

With the information now available it is possible to construct a tentative *modus operandi* for competition in determining the survival of hatchery fish:

When a group of hatchery trout is released into a body of water already occupied with fish (trout, usually) of very similar habitat requirements, the classical Darwinian setting for competition is achieved. And this is true whether or not the introduced and resident fishes are of the same species. Solomon's (1949) concepts of active struggle and prior occupancy are also realized. The niches are mostly occupied and a fairly rigid social order is established among the resident trout. When hatchery fish are introduced to this society they must find a suitable niche as well as a food supply. This involves first filling any vacant niches; if there are not enough of these the losers in the game of "musical chairs" must seize a suitable niche by aggressive action. The experimental evidence indicates that this is no easy task. Thus wild Gorge Creek trout superimposed on resident trout lower down in the same stream suffered a loss of weight for about 30 days before they established themselves and began gaining. The rôle of natural selection is clear at this point: hatchery trout lost more weight and suffered high mortalities under these circumstances. Trout partly hatchery- and partly stream-reared were intermediate in weight loss and mortality.

The above interpretation is supported by the oft-repeated observation at Gorge Creek: superimposed trout remain out in the open, in schools, clearly visible to the observer for two to four weeks after release. Similar trout, in the same stream, but after removal of resident trout, entirely disappear within one hour of release.

In the stream then, the hatchery trout is faced with two problems, finding food and finding a home. It must compete for both with resident trout. During the early period of this competition the hatchery fish are forced to remain in the current. Here they suffer from accumulation of blood lactate due to the constant muscular effort in maintaining their position. A common observation is that plants of hatchery fish in populated streams drift, in a body, downstream. At this time the weaker fish succumb. What causes death is not yet established. It might be from general acidosis, or it might be the exhaustion of an essential metabolite faster than the fishes' powers of replacing it from the food supply. It is clear that, if this is the case, competition for food may become a crucial factor in survival.

The results of the lactic acid determinations on the Gorge Creek fish show what happened *only in those fish that survived*. Because the fish were tagged, they were individually recognizable and it so happened that only two of the fish used for blood samples subsequently died. Therefore the findings are biased in favour of the tougher fish. It is quite possible that the dying fish never managed to replace their metabolites and so actually died of starvation.

This explanation of the operation of competition is particularly fitted to stream dwelling fishes where the forces of the environment causing fatigue are much more potent than in lakes. However, it does not seem necessary to postulate a different mechanism in still water. The struggle for niches, the aggressive action of resident fish, would be the same. One would expect fewer planted fish to die, and the deaths should be spread over a longer period; and, indeed, these two differences are commonly observed in lake plantings.

From the practical point of view of the fishery manager, this theory of competition should offer some useful suggestions: good survival of hatchery stock should be obtained where heavy fishing pressure has materially reduced the resident trout; "rehabilitation" of lakes by poisoning resident populations should also include resident populations of desirable species (i.e., species normally stocked) when they are not providing satisfactory angling.

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Redescription of *Lampetra ayresii* (Günther) of Western North America, a Species of Lamprey (Petromyzontidae) Distinct from *Lampetra fluviatilis* (Linnaeus) of Europe^{1,2}

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ABSTRACT

Lampetra ayresii (Günther), a species of parasitic river lamprey endemic to western North America, is redescribed on the basis of material from off the Skeena River, British Columbia, to San Francisco Bay, California. A neotype is designated. Transformed specimens differ from those of the European *Lampetra fluviatilis* (Linnaeus) in having a larger eye, a longer prebranchial and a shorter branchial region, and possibly a lower second dorsal fin, an acute rather than an obtuse caudal fin, a higher average number of trunk myomeres, and an area of dark pigment on the caudal fin. Ammocoetes differ from those of *Lampetra fluviatilis* principally in having a higher number of myomeres, a dark caudal spot (which distinguishes them also from ammocoetes of *Lampetra planeri* (Bloch), the nonparasitic brook lamprey), and an absence of dark pigment on most parts of the head and on the precursor of the tongue. Specimens from Oregon are recorded for the first time. Specimens from Mill Creek, Tehama County, California, show that this species ascends the Sacramento River farther than previous records indicated. An annotated synonymy is included. *Lampetra ayresii* is indicated as distinct from *Ammocoetes cibarius* Girard, which is regarded as identical with *Entosphenus tridentatus* (Richardson). *Lampetra ayresii* and *Lampetra fluviatilis* are illustrated by a number of original drawings and photographs.

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INTRODUCTION

ORIGINAL DESCRIPTION

More than a century ago, William O. Ayres (1855a) described from California a new species of river lamprey under the name *Petromyzon plumbeus*.

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²Contribution No. 56, Department of Fisheries, Quebec, P.Q., Canada.

His study was based on the examination of one small specimen $4\frac{3}{4}$ inches (121 mm.) long. It was taken in San Francisco Bay in November 1854. This slender lamprey was "of a plain, uniform lead colour, inclined to green, above; bright silvery beneath". According to Ayres, this specimen had "*eyes large, distant twice their own diameter from the anterior border of the head*". (It is not clear from what point on the head Ayres measured the "anterior border".) From its large eyes and small size one can judge that it was a newly transformed specimen in the macrophthalmia stage. The teeth were probably not yet cornified. Probably for this reason Ayres considered its teeth as "appendages". The following quotation is his description of the all-important teeth:

"The appendages, commonly described as 'teeth', are only two, near the lips, one superior, and one inferior, both elongated transversely. The superior is low in the middle, and elevated to a point at each end, causing it at first sight to appear double. The inferior is serrated, having eight or nine smooth nearly even points. In the throat is a partial, smooth, horny, ring or rather ridge."

The rather brief original description of *Petromyzon plumbeus* was supplemented by Bean (1887, p. 375), who stated that *Lampetra plumbea* (Ayres) has 8 cusps on the "mandibular plate" [i.e., infraoral lamina] and 3 lateral teeth [or circumorals] on each side of the disc, the median one distinctly tricuspid, and the others bicuspid.

PURPOSE OF PRESENT ARTICLE

The purpose of the present article is threefold: to present a redescription of *Lampetra ayresii* (Günther), from the rather extensive material now available; to designate a neotype of that species in place of the holotype, which has been lost; and to show that *Lampetra ayresii* (Günther), which has been relegated to the synonymy of the European *Lampetra fluviatilis* (Linnaeus), is a distinct species.

NOMENCLATURE

Because of the fact that Shaw (1804, p. 263) had already used the name *Petromyzon plumbeus* for a European lamprey, Günther (1870, p. 505) substituted for the junior homonym *Petromyzon plumbeus* Ayres the name *Petromyzon ayresii*.

We retain the termination *-ii*, which was used in the original publication of the specific name *ayresii*. The 1953 Copenhagen Congress rendered a decision to the effect that the terminations *-i* and *-ii* in a specific patronym are permissible variants, the differences between them being without nomenclatural significance (Hemming, 1953, p. 54). From recent correspondence with the Secretary to the International Commission on Zoological Nomenclature, it appears that the wording actually employed in that decision is such that *-i* and *-ii* are to be regarded as permissible variants at the time of the original publication of the name, but that, once such a name has been published, the original spelling, whether with the termination *-i* or *-ii*, is the Valid Original Spelling and is not subject to change.

We have considered the possibility that the specific name *cibarius* Girard, 1858, rather than the specific name *ayresii* Günther, 1870, might have to be

used for the lamprey that we redescribe in this paper. Creaser and Hubbs (1922, p. 13) stated, "*Ammocoetes cibarius* Girard was described as having the dorsal fins separated, and hence was probably based on either *Entosphenus t. tridentatus* or *Lampetra fluviatilis*." If *Ammocoetes cibarius* were based on the lamprey referred by Creaser and Hubbs to *Lampetra fluviatilis* (= *Lampetra ayresii* as restricted by us), we should have to use the specific name *cibarius* because of its priority. With this possibility in mind, the senior author, on June 20-21, 1957, examined a specimen at the United States National Museum which is apparently the holotype of *Ammocoetes cibarius*. It was in a jar labeled (on the outside) "No. 6176 *Am. cibarius*, Puget Sd., Dr. Suckley". Inside the jar was a label on which was written in India ink, "This is apparently type No. 981, having been recatalogued under 6176. *Ammocoetes cibarius* Type/J.V.S.". The specimen was in a rather poor state of preservation. Its tail was missing, and the skin over the branchial region was detached. Its body proportions, so far as ascertainable, were found to agree with those of a transforming ammocoete of *Entosphenus tridentatus* with which it was compared. Also, both specimens so compared had dark pigment on the lower surface around the mouth. Furthermore, Girard (1858, p. 384) stated of *Ammocoetes cibarius*, "The caudal region is dark above and below. The fins are likewise dark." We therefore conclude that *Ammocoetes cibarius* Girard is to be synonymized with *Entosphenus tridentatus* (Richardson).

METHODS OF MEASUREMENTS AND COUNTS

All measurements and counts are typically made on the left side of the specimen.

MEASUREMENTS

In the present publication we use the same measurements as those described in a previous paper by Vladykov (1955, p. 215), with the addition of one new measurement, that of the *postorbital length* (O-B₁). A brief explanation of the abbreviations used throughout the text is given below:

ABBREVIATION

EXPLANATION

a-C	<i>Tail length</i> , the distance from the posterior edge of the cloacal slit to the extremity of the caudal fin.
B ₇ -a	<i>Trunk length</i> , the distance from the posterior edge of the last (7th) branchial opening to the anterior edge of the cloacal slit.
B ₁ -B ₇	<i>Branchial length</i> , the distance from the front of the first gill opening to the posterior edge of the last (7th) gill opening.
d	<i>Disc length</i> , measured longitudinally when the disc is closed, with the oral fimbriae included.
d-B ₁	<i>Prebranchial length</i> , the distance from the anterior edge of the disc (in transformed individuals) or of the upper lip (in ammocoetes) to the anterior edge of the first branchial opening.

- hD₂ *Maximum height* of the second dorsal fin, measured along the highest fin ray.
- O *Eye length*, the horizontal diameter of the eye.
- O-B₁ *Postorbital length*, the distance from the posterior edge of the eye to the anterior edge of the first branchial opening.
- TL *Total length*, measured from the most anterior tip of the oral fimbriae to the end of the caudal fin.

All measurements are expressed in percentages of the total length of the specimen. Moreover, the disc length is expressed also in percentage of the branchial length, and the eye length in percentage of the postorbital length.

COUNTS

TRUNK MYOMERES

We follow the practice of American authors, such as Hubbs and Trautman (1937) and Vladyskov (1955), in counting *only* the trunk myomeres between the last (7th) gill-opening and the anterior edge of the cloacal slit.

TEETH

A cusp distinctly divided at its tip is counted as 2. It should be kept in mind that, regardless of the species, only half-grown transformed lampreys exhibit well-developed teeth on the disc. Spawning individuals, which are much more easily caught, are not suitable for an accurate study of the dentition, as their teeth are often worn or may even have been lost.

To clarify the references to the various types of teeth, we have added an original schematic drawing of the disc of the Pacific lamprey *Entosphenus tridentatus* (Fig. 1). We follow Hubbs and Trautman (1937, p. 32) in using the terms *transverse* (instead of *anterior*) *lingual lamina*, and *longitudinal* (instead of *posterior*) *lingual laminae*.

STAGES OF MATURITY

For a convenient comparison of the degrees of gonad development, we use a numerical system, based not only on the degree of development of the gonads, but also on the degree of degeneration of the intestinal tract, and on the diminution of the space between the two dorsal fins at the onset of sexual ripening. (Our system is very close to that suggested by the Conseil Permanent International pour l'Exploration de la Mer (1931, p. 117) for the classification of gonad maturity in the herring. We, however, refer immature specimens to Stage 0 rather than to Stage 1. For details on stages of maturity in Salmonidae, see Vladyskov, 1956.) In brief, the stages of maturity for either sex are as follows:

Stage 0.—*Immature specimens*: at least $\times 60$ magnification required to distinguish sex cells; intestine functional in parasitic species.

Stages 1, 2, and 3.—*Progressive development of gonads*: sex cells distinguishable at lower magnifications; intestine still functional; dorsal fins widely separated.

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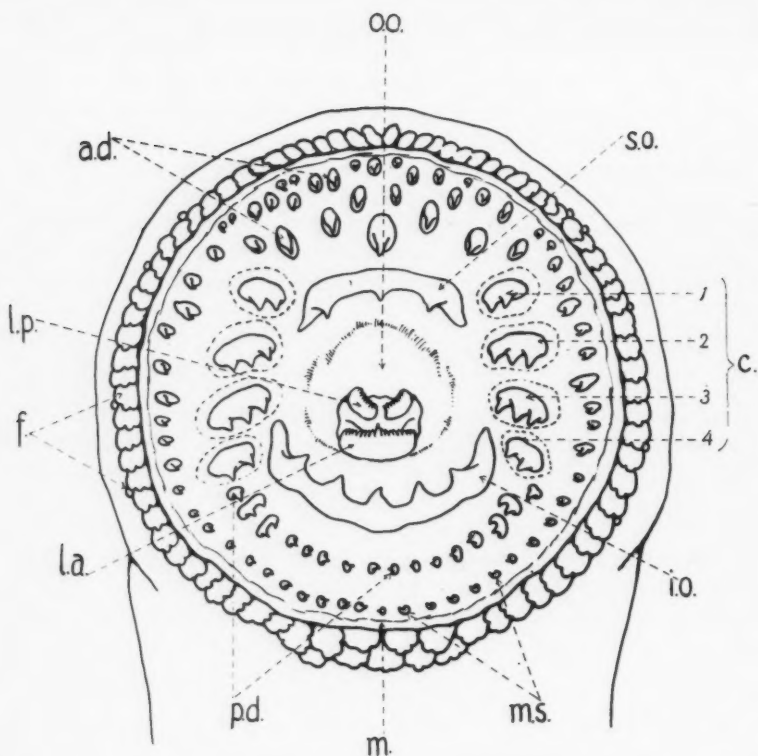


FIG. 1. Schematic drawing of the disc and dentition in the Pacific lamprey *Entosphenus tridentatus*. The significance of the abbreviations used in this drawing and in Figures 3 and 4 is as follows:

- a.d.—maxillary labials or rows of cusps of the anterior field
- c.—four circumorals or enlarged laterals
- f.—oral fimbriae or leathery marginal appendages
- i.o.—infraoral lamina or infraoral cusps
- l.a.—transverse, or anterior, lingual lamina
- l.p.—longitudinal, or posterior, lingual laminae
- m.—marginal membrane
- m.s.—marginal series or marginals
- o.o.—oesophageal opening
- p.d.—mandibular labials or row (rows) of cusps of the posterior field
- s.o.—supraoral lamina or supraoral cusps

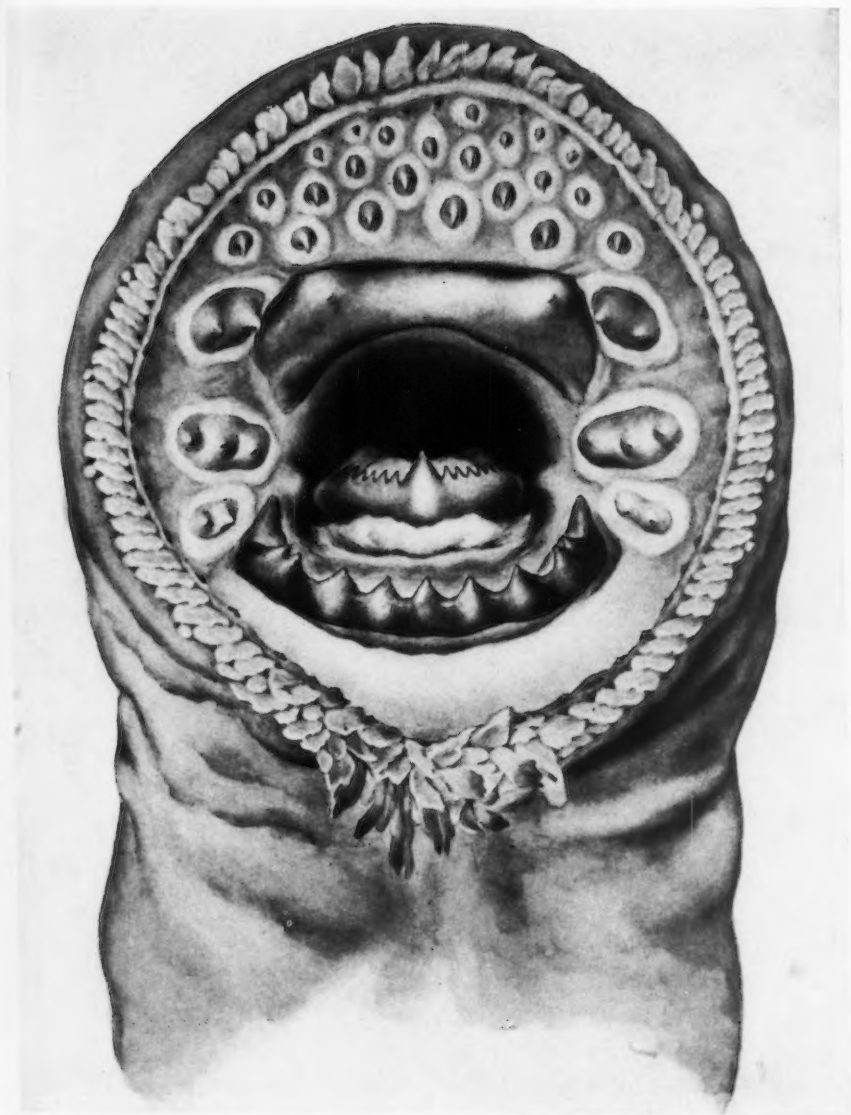


FIG. 2. Disc of the neotype of *Lampetra ayresii*, 3819B, female, TL 147 mm., San Francisco Bay, California (same specimen as shown in Fig. 5 and 6).

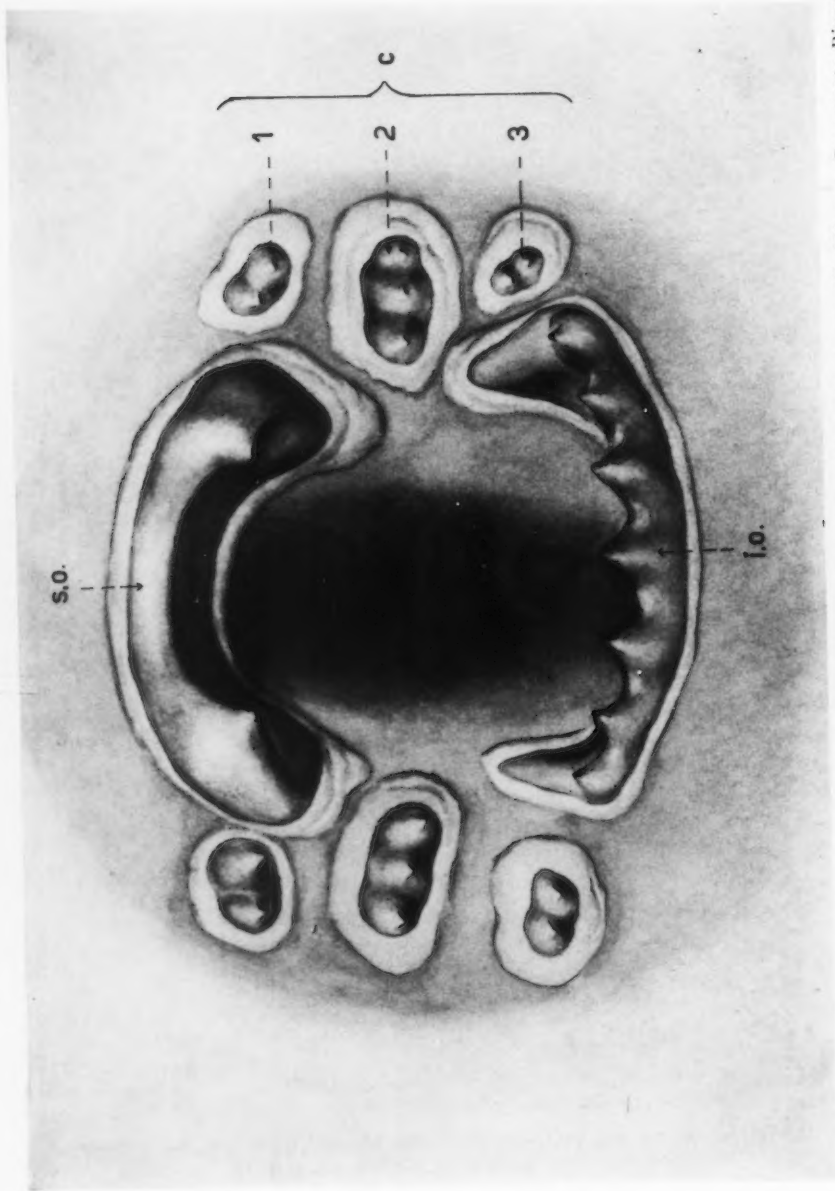


FIG. 3. Principal teeth, other than the longitudinal lingual, of *Lampetra ayresii*, 4407R, female, TL 220 mm., Sacramento River, California (same specimen as shown in Fig. 4). (For explanation of abbreviations see Fig. 1.)

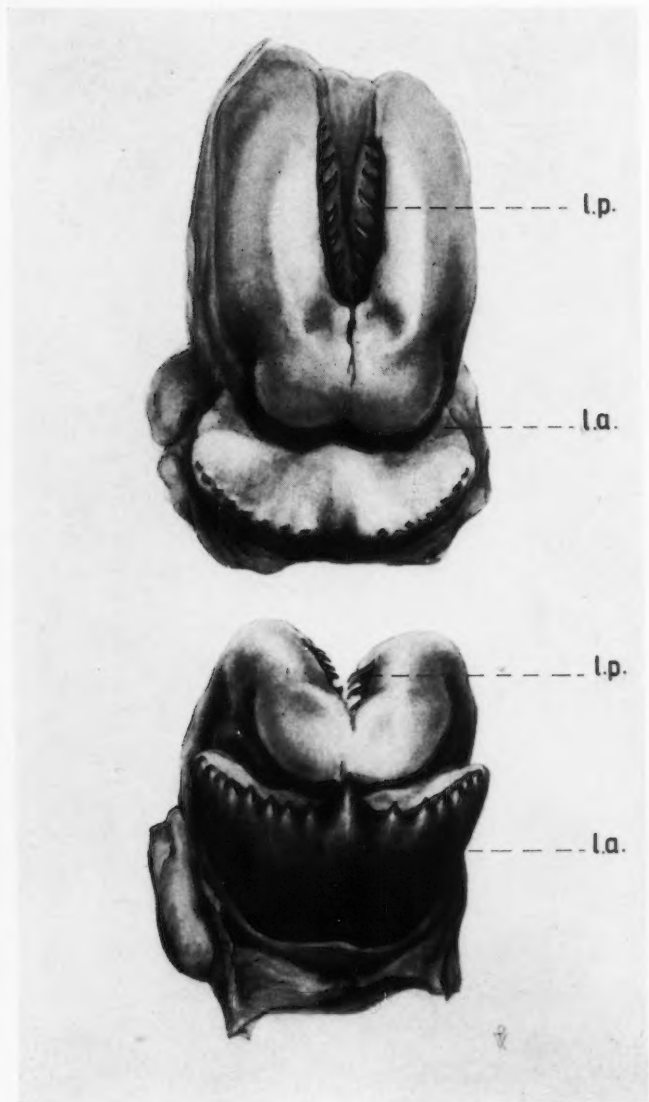


FIG. 4. Lingual teeth of *Lampetra ayresii*, 4407R, female, TL 220 mm., Sacramento River, California (same specimen as shown in Fig. 3). (For explanation of abbreviations see Fig. 1.)



FIG. 5. Lateral view of the head of the neotype of *Lampetra ayresii*, 3819B, female, TL 147 mm., San Francisco Bay, California (same specimen as shown in Fig. 2 and 6).

FIG. 6. Lateral view of the posterior two-fifths of the neotype of *Lampetra ayresii*, 3819B, female, TL 147 mm., San Francisco Bay, California (same specimen as shown in Fig. 2 and 5).



FIG. 7. Heads of young transformed specimens of *Lampetra ayresii* and *Lampetra fluviatilis*:
 a. *L. ayresii*, 2622V, male, TL 163 mm., Skeena River, British Columbia (same specimen as shown in Fig. 9a)
 b. *L. fluviatilis*, 3803B, male TL 108 mm., Crake River, England (same specimen as shown in Fig. 9b).
 Note the difference in the size of the eye.



FIG. 10. Three spawning specimens of *Lampetra ayresii*, Sacramento River, California:

a. Female, 4403R, TL 172 mm.

b. Male, 4401R, TL 181 mm. (same specimen as shown in Fig. 12a and 13a)

c. Male, 4404R, TL 194 mm.

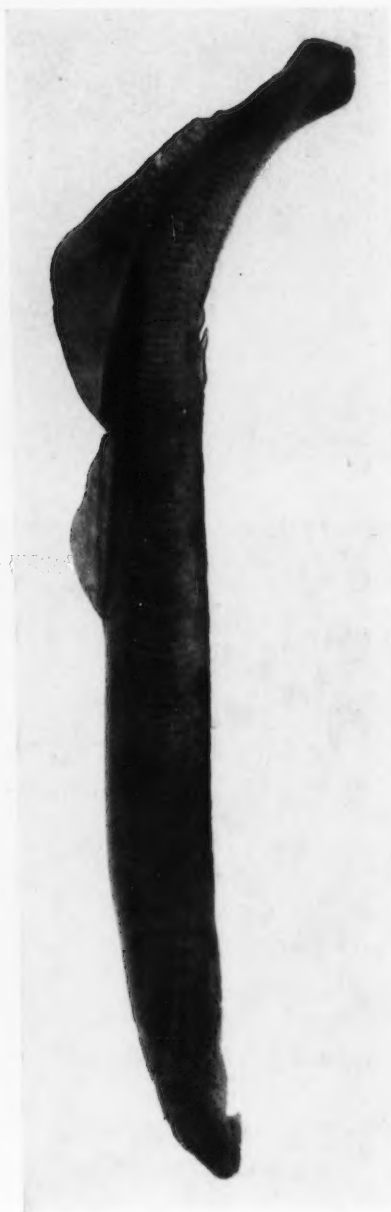


FIG. 11. Spawning male of *Lampetra fluviatilis*, 3964V, TL 253 mm., Bela River, England (same specimen as shown in Fig. 12b and 13b)



FIG. 12. Posterior half of the body of spawning males of *Lampetra ayresii* and *Lampetra fluviatilis*:
 a. *L. ayresii*, 4401R, TL 181 mm., Sacramento River, California (same specimen as shown in Fig. 10b and 13a)
 b. *L. fluviatilis*, 3964V, TL 253 mm., Bela River, England (same specimen as shown in Fig. 11 and 13b).

Note the differences in pigmentation and in the posterior angle of the caudal fin.

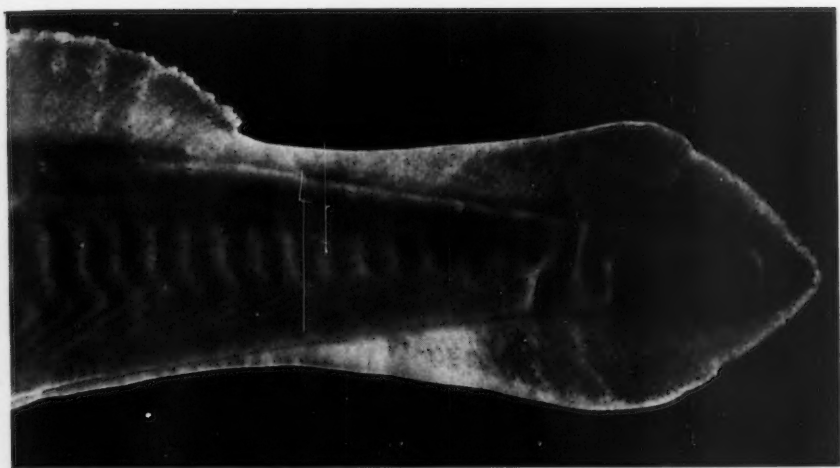


FIG. 13. Tails of spawning males of *Lampetra ayresii* and *Lampetra fluviatilis*:

- a. *L. ayresii*, 4401R, TL 181 mm., Sacramento River, California (same specimen as shown in Fig. 10b and 12a)
- b. *L. fluviatilis*, 3964V, TL 253 mm., Bela River, England (same specimen as shown in Fig. 11 and 12b).

Note the differences in pigmentation and in the shape of the caudal fin.

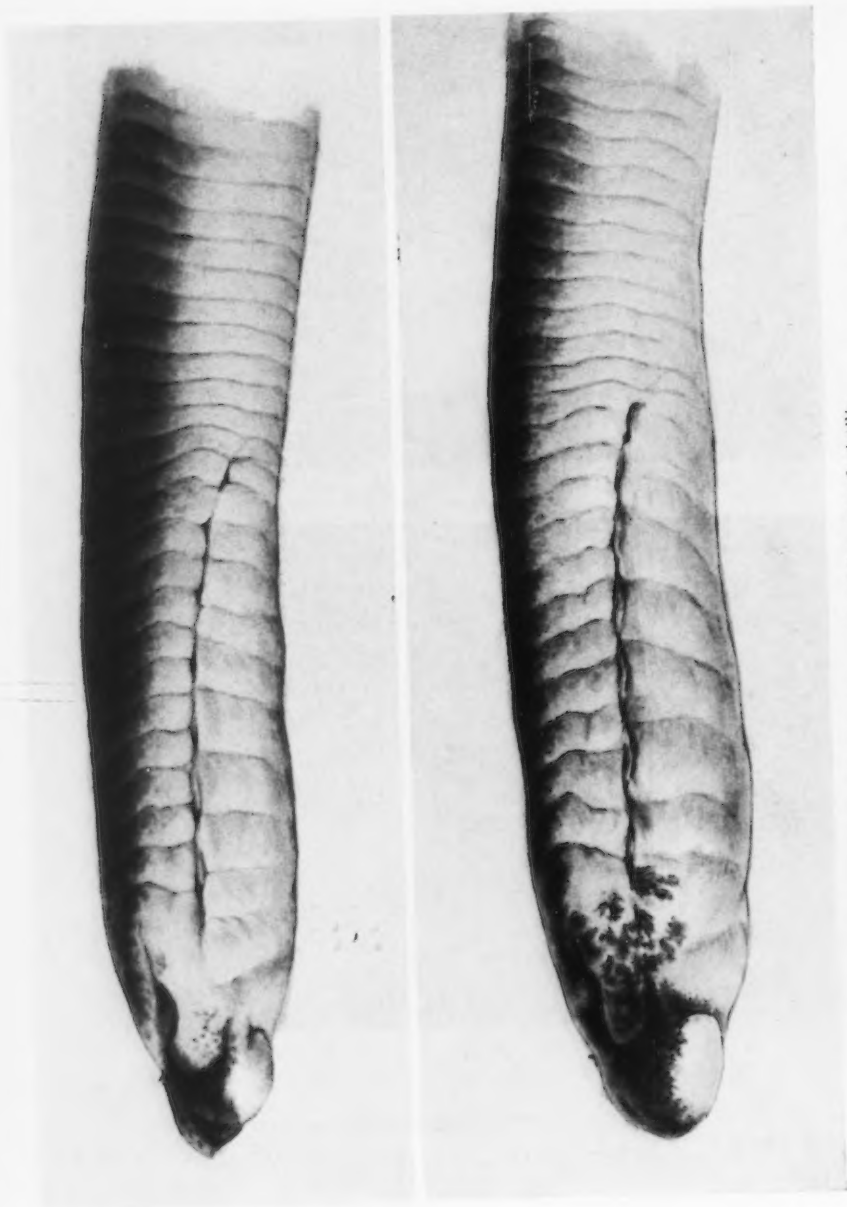


FIG. 14. Heads of ammocoetes of *Lampetra ayresii* and *Lampetra fluvialtilis*:
 a. *L. ayresii*, 3970V, TL 146 mm., Sacramento River, California (same specimen as shown in Fig. 15a)
 b. *L. fluvialtilis*, 3876B, TL 106 mm., Elnenka River, U.S.S.R. (same specimen as shown in Fig. 15b).

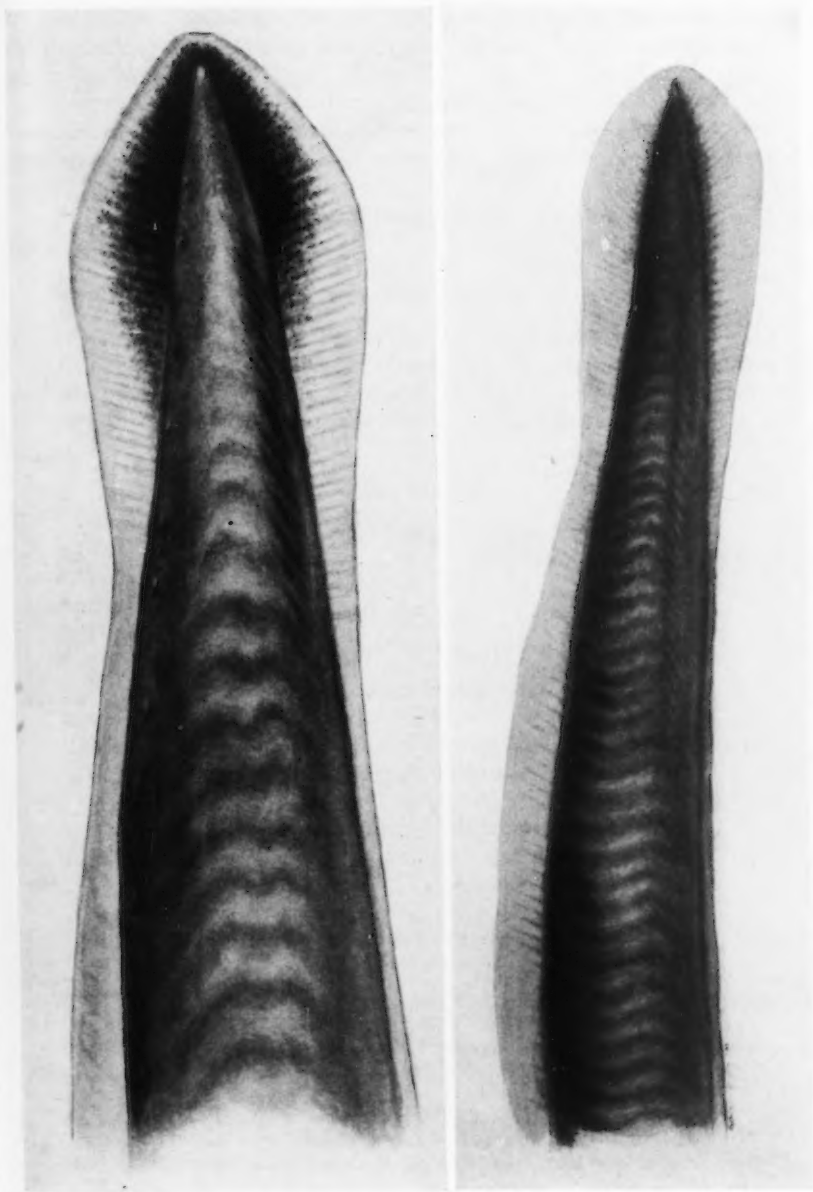


FIG. 15. Tails of ammocoetes of *Lampetra ayresii* and *Lampetra fluvialilis*:
 a. *L. ayresii*, 3970V, TL 146 mm., Sacramento River, California (same specimen as shown in Fig. 14a)
 b. *L. fluvialilis*, 3876B, TL 106 mm., Elmenka River, U.S.S.R. (same specimen as shown in Fig. 14b).
 Note the difference in pigmentation.

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Stage 4.—*Prespawning*: sexual products easily distinguishable by naked eye; intestine nonfunctional and greatly reduced; space between dorsal fins beginning to diminish.

Stage 5.—*Spawning*: sexual products occupying entire body cavity; products extruded by slight pressure on abdomen; intestine at its maximum degeneration; the two dorsal fins meeting each other; an "anal fin" present in females; a genital papilla protruding in males.

Stage 6.—*Postspawning*: body cavity empty of sexual products; specimens dying.

MATERIAL EXAMINED

Data (if known) for each collection appear in the following sequence:

1. Tag number of the Department of Fisheries, Quebec. (The letters DPQ signify a stainless-steel tag; the letter B (= blanc), J (= jaune), R (= rouge), or V (= vert) indicates the colour (white, yellow, red, or green) of a vinylite tag.)
2. Number of specimens (if more than one).
3. Sex (if transformed specimen).
4. Total length.
5. Locality.
6. Host.
7. Date of collection.
8. Collector.
9. Name of repository museum, abbreviated as follows:
CAS, California Academy of Sciences
MCZ, Museum of Comparative Zoology at Harvard College
USNM, United States National Museum
UW, University of Washington, Seattle
VM, British Columbia Provincial Museum, Victoria.
10. Catalogue number in the repository museum.

Lampetra ayresii

BRITISH COLUMBIA

2622V (♂, 163 mm.): Skeena River, off Cassiar Cannery wharf; attached to 92-mm. coho fingerling; July 16, 1955; A. Miller.

4623R (♀, 235 mm.): Discovery Island (2 miles offshore); from gullet of lingcod; Oct. 17, 1942; G. Morrel; VM 542.

WASHINGTON

3548V (♀, 311 mm.): Lake Sammamish; Oct. 12, 1949; Stephan B. Fallert.

4584R (♂, 158 mm.): Puyallup River mouth; June 22, 1940; UW 6194.

4586R (♂, 279 mm.): Lake Washington, near Seattle; attached to kokanee; Dec. 15, 1950; UW 10729.

OREGON

1320B (♂, 281 mm.): Columbia River, Bonneville; March 1940; R. Dimick.

1321B (♀, 211 mm.): Yaquina Bay; Nov. 14, 1949; E. P. Haydu and G. Watson.

CALIFORNIA

1523J-1525J (3 ♂, 197-205 mm.), 1526J-1530J (8 ammocoetes, 86-151 mm.): Mill Creek, near Los Molinos, Tehama Co.; 1954-1955; Millard Coots.

4400R-4407R (3 ♂, 5 ♀, 168-236 mm.), 4408R (ammocoete, 102 mm.): Sacramento River, near Meridian, Sutter Co.; April 28-29, 1954; E. D. Bailey.

947B (ammocoete, 146 mm.): Sacramento River, Cache Slough, Solano Co.; Jan. 20, 1954; G. W. McCammon and V. Catania.

701V (♀, 205 mm.), March 11, 1947; 702V (♂, 183 mm.), March 17, 1947; 703V-713V (5 ♂, 6 ♀, 117-155 mm.), 1391B-1392B (2 ammocoetes, 152-158 mm.), Dec. 24-31, 1948; 714V-725V (5 ♂, 7 ♀, 139-183 mm.), Jan. 17, 1949; 726V (♂, 150 mm.), 729V and 3968V-3972V (6 ammocoetes, 146-172 mm.), Jan. 14-Feb. 15, 1949; 727V-728V (2 ♀, 126-135 mm.), Feb. 25, 1949; 3955V-3963V (5 ♂, 4 ♀, 131-174 mm.), Jan. 4, 1949: Sacramento River, Isleton, Sacramento Co.; U.S. Fish and Wildlife Service; CAS 26262-26268.

3990R-3993R (1 ♂, 3 ♀, 128-179 mm.), Nov. 4, 1946; 3994R (♀, 164 mm.), Dec. 3, 1946; 3995R (♂, 171 mm.), Jan. 9, 1947; 3996R (♂, 167 mm.), Jan. 10, 1947; 3997R (♂, 157 mm.), Jan. 29, 1947; 3998R (♀, 209 mm.), Jan. 31, 1947; 3999R (♂, 220 mm.), Feb. 3, 1949: Sacramento River, at or near Rio Vista, Solano Co.; U.S. Fish and Wildlife Service; CAS 26269-26275.

1500J-1503J (4 ammocoetes, 143-161 mm.): Middle River, near Mossdale, San Joaquin Co.; May 5, 1948; U.S. Fish and Wildlife Service; CAS 26276.

1505J (♀, 120 mm.), March 18, 1947; 1506J (♂, 123 mm.), Apr. 22, 1947: San Joaquin River; U.S. Fish and Wildlife Service; CAS 26277-26278.

1507J (♀, 204 mm.), Jan. 29, 1947; 1508J (♂, 146 mm.), Jan. 31, 1947; 1509J (♂, 158 mm.), Feb. 19, 1947: San Joaquin River, Delta-Mendota Canal (?); U.S. Fish and Wildlife Service; CAS 26279-26281.

No tag number (7 transformed, 123-196 mm.): San Pablo Bay; May 1891; C. H. Townsend; USNM 67264.

No tag number (young transformed, 116 mm.): San Francisco; D. S. Jordan; USNM 27403.

700V (♂, 199 mm.): San Francisco Bay; March 2, 1955; John Reis; CAS 26261.

4615R (♂, 213 mm.): San Francisco Bay, Potrero Point, Pacific Gas and Electric Company intake, San Francisco Co., lat. 37° 45' 21" N., long. 122° 22' 53" W.; Dec. 24, 1945; D. A. Simpson; CAS 18271.

3819B (♀, 147 mm.): San Francisco Bay, Point Richmond, Parr Terminal, Contra Costa Co., lat. 37° 54' 35" N., long. 122° 23' 12" W.; Feb. 7, 1954; W. I. Follett and Ben Yacorzynski; CAS 25935; neotype.

Lampetra fluviatilis

SWEDEN

3611V-3612V (♂, ♀, 273-278 mm.), 3623V (ammocoete, 97 mm.): Dalälven River; 1955; G. Edman.

3825B-3831B (7 ammocoetes, 46-130 mm.): Lule Älv River (upper tributary); July 1955; K. Müller.

SOVIET UNION

3870B-3873B (3 ♂, 1 ♀, 295-332 mm.): Neva River; September 1948; Zoological Institute, Academy of Sciences, U.S.S.R.; 3871B = CAS 26282.

3874B-3879B (6 ammocoetes, 65-116 mm.): Elmenka River system of Baltic Sea, 4 km. from mouth; May 30, 1930; A. G. Smirnov; Zoological Institute, Academy of Sciences, U.S.S.R.; 3875B = CAS 26283.

6010B-6012B (2 ♂, 1 ♀, 265-285 mm.): indefinite locality; MCZ 26573.

POLAND

927B-946B (20 ammocoetes, 80-145 mm.): Vistula River, at Torún; May 27, 1956; Matilda Gązowska; Zoological Institute, Polish Academy of Sciences, Warsaw.

CZECHOSLOVAKIA

2011DPQ (♂, 123 mm.): Vltava River system, Voznický potok; 1947; V. Landa.

3820B-3821B (♂, ♀, 325-341 mm.): probably same locality as 2011DPQ; Ota Oliva.

NETHERLANDS

3520V-3539V (9 ♂, 11 ♀, 290-386 mm.): Meuse River, at Woudrichem; November 1949; H. Damas.

BELGIUM

3540V-3546V (6 ♂, 1 ♀, 276-325 mm.): Grande Nèthe River (tributary to Escaut (Scheldt) River), at Westerloo; April 30, 1955; H. Damas.

ENGLAND

1409J-1424J (11 ♂, 5 ♀, 239-309 mm.): Severn River, Gloucestershire; November 1951; E. W. Baxter.

3803B-3805B (3 ♂, 108-114 mm.), 3816B-3818B (3 ammocoetes, 56-104 mm.): Crake River, near Coniston Lake, N. Lancashire; March 1952; Winifred E. Frost.

3964V-3967V (4 ♂, 253-297 mm.): Bela River, 2 miles from its entrance to Kent River, South Westmorland; April 5, 1954; F.B.A. Laboratory technicians; 3966V = CAS 26284.

SYNONYMY

Petromyzon plumbeus (not of Shaw, 1804: 263).—Ayres, 1855a: [2] (original description; type locality, San Francisco Bay); 1855b: 28 [1855a repeated]; Girard, 1858: 380 (diagnosis; reference; comparisons; holotype, No. 977 [U.S. National Museum], from San Francisco Bay, California); Gill, 1862: 331 (synonym of *Lampetra plumbea*); Günther, 1870: 505 (references; synonym of *Petromyzon ayresii*); Ayres, 1873: 27 [1855a reprinted]; Jordan and Fordice, 1885: 293, 295 (synonym of *Ammocoetes cibarius*; preoccupied by Shaw); Jordan, 1887: 792 (preoccupied by Shaw, 1805); Rutter, 1908: 120 (reference; synonym of *Lampetra cibaria*); Creaser and Hubbs, 1922: 12 (synonym of *Lampetra fluviatilis*); Berg, 1931: 112 (synonym, in part, of *Lampetra fluviatilis*); Evermann and Clark, 1931: 10 (references; synonym of *Lampetra ayresii*; 48 (reference; preoccupied); 60 (reference; synonym of *Lampetra ayresii*; San Francisco).

Lampetra plumbea.—Gill, 1862: 331 (*Petromyzon plumbeus* a synonym); Cooper, 1868: 498 (California); Jordan and Gilbert, 1883: 7, 8 ("lead-colored lamprey"; description; scarcely distinguishable from the European *L. fluviatilis*; synonymy [in part]; Pacific coast); Bean, 1887: 375 (dentition; comparisons).

Ammocoetes plumbeus.—Jordan, 1878: 413 (California); Jordan and Gilbert, 1883: 867 (relationship); Evermann and Clark, 1931: 19 (reference; synonym of *Lampetra ayresii*).

Ammocoetes cibarius.—Günther, 1870: 505 (references; possible synonym of *Petromyzon ayresii*); Jordan and Fordice, 1885: 290-291 (characters in key); 292-293 (synonymy [in part]; *Ammocoetes cibarius* larva of same species; *Petromyzon plumbeus* Ayres preoccupied; Frazer's River to Sacramento River; 7-inch specimens from near Walla Walla); 295 (reference); 296 (relationships); Jordan, 1887: 792 (anadromous; *Petromyzon plumbeus* preoccupied; California); [?]Eigenmann and Eigenmann, 1892: 351 (San Francisco and Puget Sound); Creaser and Hubbs, 1922: 13 (reference; possible synonym of *Lampetra fluviatilis*).

Lampetra cibaria.—Jordan and Evermann, 1896a: 13 (characters in key; description; synonymy [in part]; Fraser River to Sacramento River); 1896b: 212 ([in part] Fraser River to Sacramento River); Evermann and Goldsborough, 1907: 91 (*Petromyzon ayresii* a synonym; British Columbia); [?]Fowler, 1908: 464 (San Francisco market); Rutter, 1908: 118 (characters in key); 119 (distinguishing character); 120, 149 ("Western brook lamprey"; synonymy [in part]; description; reference; specimen from Sacramento River at mouth of Feather River); [?]Starks, 1911: 206 (Puget Sound); Halkett, 1913: 39 ("brook lamprey"; fluviatile; parasitic; British Columbia to Sacramento River, California); Meek, 1916: 26 (not strongly differentiated; Fraser River to Sacramento River); [?]Fowler, 1923: 279 (Lakelae [Lakelse?] River [British Columbia]); Halkett, 1929: 6 ("brook lamprey"; diagnosis; Fraser River, British Columbia, to Sacramento River, California); [?]Bonnot, 1932: 16 ("lamprey"; rarely taken in Chinese shrimp nets in San Francisco Bay).

Petromyzon ayresii.—Günther, 1870: 505 (substitute name for *Petromyzon plumbeus*, preoccupied; diagnosis; *Ammocoetes cibarius* possibly a synonym; records; British Columbia); Evermann

- and Goldsborough, 1907: 91 (reference; synonym of *Lampetra cibaria*); Creaser and Hubbs, 1922: 12 (synonym of *Lampetra fluviatilis*).
- Lampetra ayresii*.—Jordan, Evermann, and Clark, 1930: 10 ("Western lamprey"; very close to *L. fluviatilis* of Europe; synonymy; Fraser River to Sacramento River); Evermann and Clark, 1931: 10 (reference; *Petromyzon plumbeus* a synonym); Schrenkeisen, 1938: 8-9 ("Western brook lamprey"; diagnosis; relationship; Fraser River to Sacramento River).
- Petromyzon ayresi*.—Berg, 1931: 112 (synonym, in part, of *Lampetra fluviatilis*).
- Lampetra ayresi*.—Evermann and Clark, 1931: 19 (reference; *Ammocoetes plumbeus* a synonym); 48 ("Western brook lamprey"; *Petromyzon plumbeus* a synonym, preoccupied; San Francisco); 62 (Sacramento-San Joaquin drainage?); Withler, 1955: 15 (*Lampetra fluviatilis* a synonym, in part; records; 162-mm. specimen found attached to 92-mm. *Oncorhynchus kisutch*, in Skeena River, British Columbia); Lindsey, 1956: 5 (*Lampetra fluviatilis* a synonym, in part).
- Lampetra fluviatilis*.—Regan, 1911: 202-203 (synonymy [in part]; diagnosis; range [in part]; Russian River, California); Creaser and Hubbs, 1922: 7 (characters in key; range [in part]); 12-13 (*Petromyzon plumbeus* and *Petromyzon ayresii* synonyms; references; intergradation with *Lampetra planeri* not improbable; critical notes; *Ammocoetes cibarius* a possible synonym; San Francisco Bay and Puget Sound, doubtless ascending West Coast streams to spawn); Hubbs, 1925: 588 (relationship; parasitic); 590 (*Lampetra planeri* seemingly a degenerate relative); Hubbs, 1928: 10 ("European river lamprey"; reference; Washington); Schultz, 1929: 45 ("brook lamprey, parasitic"; Washington); 1930a: 26 (relationship; reference; parasitic; distinguishing characters; comparisons; certain lakes and streams of Pacific drainage); 1930b: 137 (Lake Washington near Seattle); Berg, 1931: 112 (possibly a synonym, in part, of *Lampetra reissneri*; possibly a distinct species; *Petromyzon plumbeus* and *Petromyzon ayresi* synonyms; Fraser River to Sacramento River); Schultz and DeLacy, 1935: 366 ("parasitic river lamprey"; synonymy; range [in part]; references; Washington records); Schultz, 1936: 130 ("river lamprey"; "lake lamprey"; characters in key; western North America); Gunter, 1942: 308 (anadromous; recorded from both fresh water and sea water; west coast of North America); Carl and Clemens, 1948: 22 (characters in key); 25 ("Western lamprey"; diagnosis; range [in part]; predaceous; records; Cultus Lake, Fraser River, and Cowichan River, British Columbia; figure); Shapovalov and Dill, 1950: 385 ("river lamprey"; California); Withler, 1955: 15 (synonym, in part, of *Lampetra ayresi*); Lindsey, 1956: 4, 5 ("river lamprey"; references; synonym, in part, of *Lampetra ayresi*; fresh water, British Columbia).
- Lampetra reissneri*.—Berg, 1931: 103-104 (synonymy [in part]); 112 (*Lampetra fluviatilis* possibly a synonym, in part).

In omitting from the foregoing synonymy *Ammocoetes cibarius* Suckley (1860a: 368; 1860b: 368); *Ammocoetes plumbeus* Jordan and Gilbert (1881a: 458; 1881b: 30); ?*Ammocoetes plumbea* Bean (1882: 93); *Lampetra cibaria* Jordan and Starks (1895: 788), Seale (1895: 852), and Kincaid (1919: 6), we follow Schultz and DeLacy (1935: 366-367), who placed those references in the synonymy of *Lampetra planeri* (Bloch).

NEOTYPE (Fig. 2, 5, 6)

The holotype of *Petromyzon plumbeus*, collected by Ayres in San Francisco Bay, California, in November 1854, and deposited as No. 977 in the United States National Museum (Girard, 1858, p. 380), has unfortunately been lost. A letter dated July 1, 1957, from Ernest A. Lachner, Associate Curator of Fishes of that museum, reads as follows: "We have checked our catalogue books and card file for *Petromyzon plumbeus*. We did have this specimen catalogued as US 977. It was apparently lost at an early date. Our books indicate that it was destroyed. There is no other data available here."

We therefore designate the following specimen (herein referred to as 3819B) as neotype: a female, 147 mm. in total length (154 mm. before preservation), deposited in the California Academy of Sciences (CAS 25935). It was collected February 7, 1954, by W. I. Follett and Ben Yacorzynski in San Francisco Bay, at the Parr Terminal, Point Richmond, Contra Costa County, California, lat. $37^{\circ} 54' 35''$ N., long. $122^{\circ} 23' 12''$ W. (computed from U.S. Coast and Geodetic Survey Chart 5532 (San Francisco Entrance), published November 1937).

Mr. Yacorzynski caught the specimen in a herring net about five feet square, tossed from the side of the wharf, at a time when large numbers of herring, *Clupea pallasii*, were depositing their spawn on algae attached to the wharf piling. The only other fishes taken on the same occasion were single examples of *Atherinops affinis affinis*, *Damalichthys vacca*, and *Micrometrus minimus*. The following ecological data were recorded: depth of water, about 8 feet; bottom, mud (?); distance from shore (gravel beach), about 100 yards; water, turbid, salt; time of capture, about 10.00 A.M.; tide, 0.9 foot at 8.57 A.M., 4.6 feet at 3.02 P.M.; water temperature, 51°F. , air temperature, 57°F. , at 12.15 P.M.

The specimen is referable to maturity stage 0. Its proportional measurements, expressed in percentages of the total length, are as follows: prebranchial length, 12.9; branchial length, 8.9; trunk length, 49.7; tail length, 25.2; maximum height of second dorsal fin, 3.7; disc length, 5.8; eye length, 3.4; preorbital length, 2.0. The disc length in percentage of the branchial length is 65.4, and the eye length in percentage of the postorbital length is 166.7. There are 63 trunk myomeres. Lines drawn tangent to the posterior margins of the caudal fin meet at an angle of approximately 84° .

The teeth comprise 22 maxillary labials, 3 circumorals on each side (the first and third, bicuspid; the second, tricuspid); the transverse lingual lamina with 6 cusps on each side of the conspicuously enlarged median cusp; the infraoral lamina with 9 cusps (the divided cusp at each end counted as 2); and the longitudinal lingual laminae with cusps $11+10 = 21$.

In life the specimen was plumbeous grey on the back and upper sides, silvery on the preorbital, postorbital, and branchial regions and on the sides of the body to a point under the posterior end of the second dorsal fin, and white on the ventral surface. The lateral-line organs were without dark pigment. The characteristic caudal spot was blackish, approximately 6 mm. long and 5 mm. high, gradually fading anteriorly, and rather sharply defined posteriorly.

The neotype bears two tags, one of white fiber tagboard impressed with the California Academy of Sciences catalogue number 25935, and the other of white laminated vinylite inscribed in black with the number 3819B on one side and the words "Département des PECHERIES Québec" on the other side.

DESCRIPTION OF *LAMPETRA AYRESII* (GÜNTHER)

The material of *Lampetra ayresii* that we have examined consists of 81 transformed individuals (37 males, 36 females, 8 undetermined) and 22 ammocoetes, not only from San Francisco Bay, the type locality, but also from several

other localities along the west coast of North America from California to British Columbia. For comparative purposes, we have examined material of *Lampetra fluviatilis*, the European river lamprey, consisting of 62 transformed individuals (41 males and 21 females) and 37 ammocoetes, from seven European countries.

DIAGNOSIS

A species of *Lampetra*³ that is distinguished from other congeneric species by having (1) a high number of trunk myomeres (averaging 68.0 in transformed individuals, and 66.8 in ammocoetes); (2) different body proportions (including large eyes); and (3) pronounced dark pigment on the tail both in ammocoetes and in transformed individuals.

COMPARISON WITH *Lampetra fluviatilis* (LINNAEUS)

TRANSFORMED SPECIMENS

TOTAL LENGTH (Tables I-V). The transformed specimens of *Lampetra ayresii* seem to average shorter than those of *L. fluviatilis*. The ranges of total length for *ayresii* examined by us are 120-311 mm. (average 168.9 mm.) in females and 117-281 mm. (average 170.8 mm.) in males; and for *fluviatilis*, 278-386 mm. (average 325.9 mm.) in females and 108-362 mm. (average 263.6 mm.) in males. Berg (1931, pp. 107, 109, 110-111; 1948, p. 44) gave the minimum size of transformed specimens of *fluviatilis* as 86 mm. and the maximum as 405 mm.

BODY PROPORTIONS (Tables I-V). The most striking of the morphometric differences between *ayresii* and *fluviatilis* is in the eye length, which, expressed as a percentage of the postorbital length, ranges in *ayresii* from 100 to 200 and in *fluviatilis* from 77 to 120 (more than 100 in only one specimen); the averages are 144.8 for *ayresii* and 88.2 for *fluviatilis*; in specimens of comparable size the eye is larger in *ayresii*, but in each species the relative size of eye decreases sharply with increased size of fish; the differences observed can be attributed in part to the smaller size of *ayresii*, at least as represented by specimens examined. The prebranchial length is greater in *ayresii* than in *fluviatilis*: range, 10.9 to 14.1% of the total length rather than 10.0 to 12.9; average, 12.5 rather than 11.6. The branchial length as a percentage of the total length averages less in *ayresii*, 9.0 versus 10.2 in females and 9.0 versus 9.8 in males; but the range is about the same, 7.8 to 11.8 in *ayresii* (both sexes) and 7.9 to 10.8 in *fluviatilis*. The height of the second dorsal fin, as a percentage of the total length, may average somewhat less in *ayresii*, perhaps because there are fewer mature specimens; the averages for females are 3.7 versus 4.7, and for males, 3.5 versus 5.2; the ranges widely overlap—for females, from 2.4 to 6.8 versus 3.7 to 6.3, and for males, from 2.3 to 6.1 versus 3.2 to 7.8.

DENTITION (Tables IX-X). In actively feeding adults of *ayresii*, all the teeth are sharp, but in spawning individuals they become progressively blunt. As is typical for all species of *Lampetra*, the mandibular labials are lacking (see Fig. 1 and 2). Of the three circumorals on each side of the disc, the middle one

³We follow Regan's (1911, p. 202) definition of the genus *Lampetra*.

is tricuspid and the others bicuspid (of 70 specimens, only one (4401R) had, on the right side of the disc, a bicuspid middle circumoral). The general pattern of dentition is very similar to that in *fluviatilis*. The number of teeth on the anterior field of the disc is somewhat higher than in *fluviatilis*, but variable. The number of cusps on the infraoral lamina (Table IX) varies from 7 to 10 and averages 8.9; in *fluviatilis* the range is the same but the average may be slightly lower (8.2 for material examined). The cusp at each end of the infraoral lamina is often bicuspid. The average number of transverse lingual cusps is 14.3 in *ayresii*, 13.3 in *fluviatilis* (Table IX). As in all species of *Lampetra*, the median cusp of the transverse lingual lamina is much enlarged (Fig. 2 and 4). The number of cusps on the longitudinal lingual laminae (Table X) appears to be smaller in *ayresii*: in six specimens the count varies from 9 to 11+9 to 12 = 19 to 22, averaging $10.2+10.5 = 20.7$, whereas in seven of *fluviatilis* the count varies from 10 to 13+9 to 13 = 19 to 26, averaging $11.3+11.1 = 22.4$ (Table X).

TRUNK MYOMERES (Tables VI–VIII). For a species of *Lampetra*, *L. ayresii* has a high average number of myomeres. In the transformed specimens examined, the counts average 68.0 in *ayresii* and 63.4 in *fluviatilis*. Although the observed ranges do not appear distinctive for transformed specimens, being 60 to 71 in 69 specimens of *ayresii* and 61 to 66 in 61 specimens of *fluviatilis*, there are fewer than 65 myomeres in only three of our specimens of *ayresii*.

COLORATION. In *Lampetra ayresii* the tail is coloured very similarly in ammocoetes and adults, the caudal fin having a permanent dark-grey pigmentation of a definite pattern (Fig. 9a and 15a). In *Lampetra fluviatilis* the caudal fin of ammocoetes (Fig. 15b) and of young adults (Fig. 9b) has no dark pigment at all, but with the onset of spawning that fin becomes rather evenly suffused with dark pigment (Fig. 13b). The other species of *Lampetra* (except *L. zanandrei*, a nonparasitic form described by Vladykov (1955) from northern Italy) resemble *L. fluviatilis* in lacking dark pigment on the caudal fin until the onset of the spawning season. In preserved specimens of *ayresii* the caudal fin is yellowish with the dark pigmentation mentioned above; the two dorsal fins are yellowish, with some dark pigment in spawning individuals.

The rows of lateral-line organs in *ayresii* remain uncoloured throughout life, as has been stated by Vladykov (1955, p. 219) to be typical of all species of lampreys having two distinct dorsal fins.

In preserved specimens of *ayresii*, the sides and back are brownish grey and the lower surface is whitish. Transformed specimens of *fluviatilis* are a uniform bluish brown on the back and sides, whitish below. According to Berg (1948, p. 44) adult specimens of *fluviatilis*, during their migration from the sea, have a metallic-bronze tinge. Apparently those of *ayresii* never acquire such coloration, but those taken in salt water are silvery on the sides.

FORM OF FINS (Fig. 12, 13). In transformed specimens the caudal fin is narrower in *ayresii* than in *fluviatilis*, and the posterior borders form a somewhat acute rather than somewhat obtuse angle. In spawning specimens the second dorsal fin is somewhat lower in *ayresii* than in *fluviatilis*.

SEXUAL DIMORPHISM. The sexual dimorphism in *ayresii* is very similar to that of other lampreys (Vladykov, 1949 and 1955). At the onset of sexual ripening, in each sex, the dorsal fins approach each other and eventually meet (Fig. 10-12). At the same time, the degeneration of the intestinal tract reaches a maximum. In our material the average disc length is similar in the sexes (Tables I, II, and V), but the disc may be somewhat enlarged in breeding males. The tails of males may average slightly longer than those of females (Table V). The height of the second dorsal fin does not appear significantly different in the sexes (Fig. 10).

LIFE HISTORY. The large disc with sharp teeth and the well-developed intestinal tract prove that *ayresii*, like *fluviatilis*, is parasitic. In fact it has been seen parasitizing kokanee in Lake Washington (4586R), and (2622V) a coho fingerling in Skeena River (Withler, 1955). Two males (4615R, 213 mm., and 700V, 199 mm.), taken in San Francisco Bay, were reported as feeding adults full of blood.

Apparently, ammocoetes of *ayresii* metamorphose at a larger size than do those of *fluviatilis*. For the latter species, Berg (1948, p. 44) mentioned transformed individuals only 86 to 102 mm. long. The smallest recorded specimen of *ayresii* is the 121-mm. specimen described by Ayres (1855a). In our material the smallest individual is a male 117 mm. long (711V).

Our specimens of *ayresii* that were nearly ready to spawn (4400R-4407R) were all taken in the Sacramento River, near Meridian, California, on April 28-29, 1954. The spawning season therefore, at least in California, probably extends from the end of April through May.

In order to present information on the fecundity of *ayresii*, we estimated the number of eggs in the ovaries of two females, using the method described by Vladykov (1951). A 175-mm. female (4402R) weighing 20.2 grams was estimated to contain 37,288 eggs 0.7 mm. in diameter (5,108 eggs per gram of ovary). In the other female (4405R), 230 mm. long and weighing 24 grams, the number of eggs, 0.6 mm. in diameter, was estimated at 11,398 (5,428 eggs per gram of ovary). The maturity index⁴ of the 175-mm. female was 36. The 230-mm. female was not yet ready to spawn, as was indicated by its low maturity index of 9.

Lampetra ayresii is obviously anadromous, as it has been found both in fresh and in salt water. Four of our specimens were taken in salt water: the neotype (3819B) and an adult male (700V) from San Francisco Bay, California; a female (1321B) from Yaquina Bay, Oregon; and a large female (4623R) from the gullet of a lingcod caught two miles off Discovery Island, British Columbia. The remaining specimens, ammocoetes and transformed, were obtained in fresh water, in the Sacramento-San Joaquin system, California, the Columbia River, Oregon, or in lakes in the State of Washington.

Lampetra fluviatilis, like *L. ayresii*, is an anadromous and parasitic species.

⁴The weight of the ovary expressed in percentage of the total weight of the specimen is called "maturity index". In certain other species of lamprey this index has been shown to average from 20 to 33, with a maximum of 47, during spawning (Vladykov, 1951, pp. 7, 9, 11).

In European rivers it undertakes regular migrations to and from the sea. Its spawning season varies regionally. In the upper Rhine, spawning has been observed from February to April (Berg, 1931, p. 113); in the British Isles, during April and May (Jenkins, 1950, p. 346); and in the lower Neva River, from the first of June to early July (Berg, 1948, p. 47).

AMMOCOETES

Pioneer studies on ammocoetes by Vladykov (1950) have shown that in addition to the body proportions and the number of myomeres, one of the most important characters for the identification of larval lampreys (which lack the disc of the adults) is the pigmentation of the head and tail regions.

TOTAL LENGTH (Tables XI–XIII). The ammocoetes of *ayresii* seem to average longer than those of *fluviatilis*. The average total length of our 22 ammocoetes of *ayresii* is 137.5 mm. and the range, 86–172 mm., against an average of 117.6 mm. and a range of 100–145 mm. in our 20 ammocoetes of *fluviatilis*.

BODY PROPORTIONS (Tables XI–XIII). The two anterior lengths, prebranchial and branchial, seem shorter in *ayresii* than in *fluviatilis*. In 12 ammocoetes of *ayresii* the observed prebranchial length as a percentage of the total length ranges from 5.9 to 8.3 (average 6.7) versus 6.8–9.3 (average 8.0) in our 20 ammocoetes of *fluviatilis*; the branchial, from 9.6 to 11.8 (average 10.5) versus 11.1–13.2 (average 12.2). The trunk and tail regions seem longer in *ayresii* than in *fluviatilis*. The range of trunk length as a percentage of the total length is 51.7 to 55.0 (average 53.4) in *ayresii* versus 49.0–53.8 (average 51.7) in *fluviatilis*, and the range of tail length, 26.5 to 28.9 (average 27.3) versus 25.2–28.5 (average 26.3).

TRUNK MYOMERES (Tables VI–VIII). The myomeres are more readily distinguishable in ammocoetes than in adults. On the average, there are 1 or 2 fewer trunk myomeres in ammocoetes than in transformed individuals of the same species. The higher number of myomeres in the specimens of *ayresii* at hand readily separates the ammocoetes of *ayresii* from those of other species of *Lampetra*. In the ammocoetes examined (19 of *ayresii*, 34 of *fluviatilis*) the counts range from 65 to 71 (average 66.8) in *ayresii* and from 58 to 64 (average 60.4) in *fluviatilis*.

COLORATION (Table X). The pattern and extent of dark pigmentation on certain parts of the head and body of the ammocoetes are very important taxonomic characters, as indicated by Vladykov (1950, pp. 83–94).

Most parts of the head of *ayresii*, including the subocular and postorbital regions, are unpigmented (Fig. 14a). The ammocoetes of *fluviatilis* all have some pigment on the subocular region (Fig. 14b), and 45 percent have pigment on the postorbital region as well.

Ammocoetes of *ayresii* and *fluviatilis* appear to differ also in the pigmentation of the "precursor of the tongue". Two ammocoetes of *ayresii* (3969V and 3971V), on dissection, show that both the bulb of the precursor and its elastic ridge are white, with no trace of dark pigment. On the other hand, two ammocoetes of *fluviatilis* (3874B and 3875B) from the Soviet Union have dark pigment

on the bulb of the precursor of the tongue and along its elastic ridge. A technique for dissecting the precursor of the tongue in ammocoetes of eastern American lampreys is described and illustrated by Vladikov (1950, pp. 90-95).

The principal difference between these two species is in the pigmentation of the caudal fin. In ammocoetes of *ayresii* there is a symmetrical dark spot on the posterior three-quarters of the caudal fin (Fig. 15a), but in those of *fluviatilis* there is no dark pigment at all on the tail (Fig. 15b). The same character distinguishes ammocoetes of *ayresii* from those of *Lampetra planeri* (Bloch). As shown by Vladikov (1955, Plate IIIb), the ammocoetes of *planeri*, like those of *fluviatilis*, have no dark pigment on the caudal fin.

DISTRIBUTION

Lampetra ayresii has been recorded from several localities on the eastern seaboard of the north Pacific, from off the Skeena River, British Columbia, to San Francisco Bay, California. Its omission by Clemens and Wilby (1946) may presumably be ascribed to a lack of definitely marine records of the species from British Columbia. The two specimens that we list from Oregon, which were contributed by Carl E. Bond, appear to constitute the first records of this species from that State. Our specimens from Mill Creek, Tehama County, California, show that this species ascends the Sacramento River much farther than was indicated by Rutter's (1908: 120) record of a specimen from the mouth of the Feather River.

Lampetra ayresii was not recorded from southern California by Barnhart (1936), nor from Alaska by Wilimovsky (1954a, b) or by Walters (1955). It was not recorded from Japan by Jordan and Snyder (1901) or by Jordan and Hubbs (1925), nor from the northern seas of the Soviet Union by Andriiashev (1954).

According to Berg (1931, pp. 111-112; 1948, p. 46), *Lampetra fluviatilis* is common in the Baltic and North Sea basins and in France and Ireland. It is found also in the Rhone, the Arno, and the Tiber Rivers, but is absent from the regions of the Black Sea and the Arctic Ocean. It does not occur at all in the Asiatic part of the Eurasian continent. The supposition that *fluviatilis* is found also along western North America is not supported by the facts presented in this paper.

INFRASPECIFIC VARIATION

Because of certain peculiarities of the western coast of North America, such as the occasional close proximity of high mountains to the sea, the fish fauna of individual rivers is often very distinct. Thus we can expect that eventually it will be possible to segregate *Lampetra ayresii* into local populations.

Berg (1948, pp. 44-53) recognized several local forms of *fluviatilis*. Our specimens of *fluviatilis* from the Netherlands and Belgium appear to differ somewhat, at least in number of myomeres, from those from England (Table VII).

SUMMARY

1. The parasitic river lamprey of western North America, *Lampetra ayresii* (Günther), is redescribed from an examination of 103 specimens taken in British Columbia, Washington, Oregon (apparently the first records from that State), and California.
2. It is established that the holotype of this species has been lost.
3. A neotype, from San Francisco Bay, California, is designated.
4. *Lampetra ayresii*, long regarded as conspecific with the European river lamprey, *Lampetra fluviatilis* (Linnaeus), is shown to be a distinct species which is known only from the eastern seaboard of the north Pacific, from off the Skeena River, British Columbia, to San Francisco Bay, California.
5. In comparing the two species, 99 specimens of *Lampetra fluviatilis* from Sweden, the Soviet Union, Poland, Czechoslovakia, the Netherlands, Belgium, and England were examined.
6. Transformed specimens of *Lampetra ayresii* are shown to differ from those of *Lampetra fluviatilis* in having a larger eye, a longer prebranchial and a shorter branchial region, and possibly a lower second dorsal fin, an acute rather than an obtuse caudal fin, a higher average number of trunk myomeres, and a characteristic area of dark pigment on the caudal fin.
7. Ammocoetes of *Lampetra ayresii* are shown to differ from those of *Lampetra fluviatilis* principally in having a dark caudal spot (which distinguishes them also from ammocoetes of *Lampetra planeri* (Bloch), the nonparasitic brook lamprey), a higher number of myomeres, and an absence of dark pigment on most parts of the head and on the precursor of the tongue.
8. Ammocoetes of *Lampetra ayresii* apparently metamorphose at a larger size than do those of *Lampetra fluviatilis*.
9. The spawning season of *Lampetra ayresii*, at least in California, probably extends from the end of April through May.
10. *Lampetra ayresii* ascends the Sacramento River at least as far as Mill Creek, Tehama County, California.
11. *Lampetra ayresii* appears to be distinct from *Ammocoetes cibarius* Girard, the holotype of which is apparently referable to *Entosphenus tridentatus* (Richardson).

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TABLE I. Body proportions (in percentages) of females of *Lampetra ayresii*.

Tag No.	Stage of maturity	TL (mm.)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$	$\frac{hD_2}{TL}$	$\frac{d}{TL}$	$\frac{d}{B_1-B_7}$	$\frac{O}{TL}$	$\frac{O-B_1}{TL}$	$\frac{O}{O-B_1}$
1505J	0	120	12.5	8.3	47.9	28.8	3.8	5.8	70.0	3.8	2.1	180.0
727V	0	126	12.7	8.7	48.0	27.8	4.0	5.6	63.6	4.0	2.0	200.0
3960R	0	128	13.3	9.0	47.7	27.4	3.9	5.9	65.2	3.9	2.0	200.0
3963V	0	131	12.6	8.8	50.4	26.3	3.4	5.3	60.9	3.4	2.3	150.0
728V	0	135	11.9	8.0	50.4	26.7	3.7	5.6	62.5	3.7	2.2	166.6
3961V	0	140	12.9	8.6	48.9	27.9	3.2	5.7	66.7	3.6	2.1	166.7
713V	0	141	12.8	8.5	48.9	27.7	3.5	5.0	58.3	3.5	2.1	166.6
723V	0	144	12.5	8.3	50.0	26.4	3.5	5.6	66.7	3.5	2.1	166.6
725V	0	145	12.4	8.6	49.7	27.3	3.4	5.5	66.7	3.4	2.1	166.6
707V	0	145	12.1	8.3	49.7	27.6	3.4	5.5	66.7	3.4	2.1	166.6
3819B	0	147	12.9	8.9	49.7	25.2	3.7	5.8	65.4	3.4	2.0	166.7
704V	0	147	12.9	8.5	48.3	28.6	3.1	5.1	60.0	3.4	2.4	142.9
710V	0	148	11.5	8.8	50.3	27.7	3.4	4.7	53.8	3.4	1.7	200.0
721V	0	148	12.1	8.5	48.7	27.7	2.7	5.4	60.0	3.4	2.0	166.6
709V	0	149	12.1	8.4	48.0	29.5	3.0	5.3	61.5	3.3	2.3	142.9
706V	1	150	12.0	8.7	51.3	26.0	3.0	5.3	65.4	3.3	2.6	125.0
3959V	0	153	13.1	8.5	49.0	28.1	3.6	5.6	65.4	3.2	2.2	142.9
724V	0	157	12.1	8.3	49.7	28.7	3.2	5.4	65.4	3.1	2.5	125.0
3957V	0	158	12.3	8.2	50.6	26.9	3.2	5.4	65.4	3.1	2.4	125.0
719V	0	162	12.4	8.0	50.3	27.8	3.7	5.2	65.5	3.0	2.4	125.0
3994R	1	164	12.8	8.9	48.8	27.7	3.4	5.8	65.5	3.0	2.4	125.0
3992R	1	165	12.1	8.5	50.0	27.9	3.3	6.1	71.4	3.0	2.4	125.0
4400R	5-6	168	13.7	10.1	51.2	26.2	6.6	6.9	67.7	3.3	2.4	137.5
4403R	5	172	12.8	9.6	52.9	24.4	6.7	—	—	2.9	2.3	125.0
716V	1	173	12.1	8.1	50.9	27.2	3.2	5.5	67.9	3.2	2.3	137.5
4402R	5-6	177	13.6	11.8	48.8	24.9	6.8	6.8	57.5	2.7	2.4	112.5
3991R	1	179	12.0	8.4	50.8	26.8	2.8	5.0	60.0	2.8	2.2	125.0
718V	1	183	11.2	8.8	50.6	27.9	3.3	4.9	56.3	3.0	1.9	157.1
1507J	3	204	11.8	9.8	50.3	26.5	3.2	5.4	46.8	2.5	2.5	100.0
701V	3-4	205	11.7	10.2	51.2	25.1	3.9	5.1	50.0	2.9	2.2	133.3
3998R	3	209	12.0	9.6	50.8	26.1	3.1	5.8	60.0	2.9	1.9	150.0
4407R	4-5	220	11.4	10.5	53.7	24.7	3.9	5.9	56.5	2.3	2.3	100.0
4405R	5	230	11.3	10.2	52.6	24.8	4.1	5.4	53.2	2.4	2.4	100.0
4023R	2	235	12.8	11.1	—	—	—	6.2	55.8	3.0	3.0	100.0
3548V	2	311	13.1	9.9	50.0	26.0	3.5	5.8	58.1	2.6	2.1	123.1
MEAN		167.7	12.4	9.0	48.6	27.0	3.7	5.6	61.9	3.3	2.2	146.2

TABLE II. Body proportions (in percentages) of males of *Lampetra ayresii*.

Tag No.	Stage of maturity	TL (mm.)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_2}{TL}$	$\frac{B_2-a}{TL}$	$\frac{a-C}{TL}$	$\frac{hD_2}{TL}$	$\frac{d}{TL}$	$\frac{d}{B_1-B_2}$	$\frac{O}{TL}$	$\frac{O-B_1}{TL}$	$\frac{O}{O-B_1}$
711V	0	117	14.1	8.6	47.0	27.4	3.4	5.6	65.0	4.3	2.1	200.0
1506J	0	123	13.8	8.1	48.8	26.8	4.1	6.1	75.0	4.1	2.0	200.0
712V	0	130	13.3	8.8	48.5	28.5	3.5	5.4	60.9	3.8	2.7	142.9
3993R	0	135	13.0	8.9	48.2	27.4	3.7	5.9	66.7	3.7	2.2	166.7
705V	0	136	13.2	10.3	47.8	26.5	2.6	5.9	57.1	3.7	2.2	166.7
3962V	0	136	13.2	9.2	47.8	26.9	3.3	6.3	68.0	3.3	2.2	150.0
3958V	0	137	12.4	8.0	49.3	28.1	2.9	5.5	68.2	2.9	2.2	133.3
722V	0	139	13.0	9.0	48.9	27.3	2.9	5.8	64.0	3.6	2.2	166.7
717V	0	140	12.5	8.6	48.2	28.9	3.2	5.0	58.3	3.6	2.1	166.6
715V	0	141	12.8	8.5	48.9	27.7	2.8	5.7	66.7	3.5	2.1	166.6
703V	0	142	13.0	9.2	47.9	28.2	3.5	5.6	61.5	3.5	2.5	142.9
1508J	0	146	13.0	8.9	49.3	26.0	2.7	6.2	69.2	3.4	2.1	166.6
726V	0	150	12.0	8.3	50.0	27.3	4.0	5.3	64.0	3.3	2.0	166.6
714V	0	154	11.7	7.8	51.0	26.9	3.2	5.2	66.7	3.2	2.0	166.6
708V	0	155	12.3	9.0	48.7	27.4	3.2	5.2	57.1	3.2	2.3	142.9
3997R	0	157	12.4	8.0	49.7	28.1	3.2	5.7	72.0	3.2	2.2	142.9
1509J	1	158	11.4	8.2	50.0	28.2	3.8	5.4	65.4	3.2	2.5	125.0
3960V	0	158	12.7	8.2	48.1	29.1	3.2	5.7	69.2	3.2	2.5	125.0
4584R	0	158	13.6	9.8	48.1	26.9	3.5	5.7	58.1	3.2	2.5	125.0
2622V	0	163	13.5	8.3	50.6	27.9	3.7	6.1	74.1	3.1	2.5	125.0
3996R	0	167	11.7	8.4	50.9	26.9	3.0	6.0	71.4	3.0	2.4	125.0
720V	1	169	12.1	8.6	50.9	26.6	2.7	5.3	62.1	3.0	2.1	142.9
3995R	0	171	12.6	8.8	49.1	27.5	2.3	5.9	66.7	2.9	2.3	125.0
3958V	2	174	12.1	9.0	49.7	27.7	3.2	5.5	61.3	2.9	2.3	125.0
3955V	0	174	12.2	8.7	51.4	26.2	3.5	4.9	56.7	3.2	2.3	137.5
4401R	5-6	181	13.3	11.1	45.9	29.3	6.1	7.2	65.0	2.8	2.5	111.1
702V	4	183	12.0	9.8	50.8	26.2	4.4	6.0	61.1	3.3	2.2	150.0
4404R	4	194	13.2	10.6	49.0	26.3	5.4	7.2	68.3	2.6	2.6	100.0
700V	2	199	—	—	—	—	—	—	—	3.0	2.5	120.0
4015R	1	213	—	9.9	55.9	25.4	3.5	—	—	—	—	—
3999R	3	220	10.9	9.3	51.0	27.3	3.2	5.5	58.5	2.7	2.1	133.3
4406R	4	235	11.1	10.6	53.8	24.7	4.2	5.1	47.1	2.3	2.1	110.0
4586R	2	279	—	—	—	—	—	6.1	—	2.5	2.2	116.7
MEAN		164.7	12.6	9.0	49.5	27.3	3.5	5.7	64.2	3.2	2.3	143.3

TABLE III. Body proportions (in percentages) of females of *Lamprologina fluvialis*.

Tag No.	Stage of maturity	TL (mm.)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_2}{TL}$	$\frac{B_2-a}{TL}$	$\frac{a-C}{TL}$	$\frac{hD_2}{TL}$	$\frac{d}{TL}$	$\frac{d}{B_1-B_2}$	$\frac{O}{TL}$	$\frac{O-B_1}{TL}$	$\frac{O}{O-B_1}$
3611V	4	278	11.5	9.4	51.8	24.5	4.1	5.9	63.5	2.2	2.3	92.3
2003DPQ	3	283	11.8	10.2	53.0	26.1	—	6.2	60.3	1.4	2.5	85.7
2002DPQ	3	285	11.9	10.5	50.7	27.5	—	6.1	58.3	1.9	2.8	68.8
6012B	4	285	10.5	10.0	53.3	24.4	—	5.8	57.9	1.8	2.1	83.3
2000DPQ	3	296	12.3	10.1	52.4	26.7	—	5.7	56.7	2.0	2.5	80.0
2016DPQ	3	305	11.3	10.5	51.1	26.6	5.3	5.9	56.3	2.0	2.3	85.7
2015DPQ	3	309	11.3	9.2	52.4	25.9	4.9	5.8	63.2	1.9	2.3	85.7
3536V	4	318	11.0	9.9	52.2	26.7	4.7	5.2	52.4	2.2	2.4	93.3
3537V	4	320	10.9	10.5	50.9	26.6	4.5	5.2	49.3	2.2	2.0	92.3
3544V	6	325	11.1	10.8	47.2	26.7	6.3	4.9	45.7	2.2	2.4	87.5
3531V	4	330	11.2	9.9	51.5	27.3	5.6	5.0	48.5	2.1	2.3	93.3
3524V	4	330	11.7	10.3	53.6	24.9	4.6	5.5	55.4	2.1	2.3	93.3
3526V	4	341	11.1	10.3	54.3	24.9	4.7	5.0	48.6	2.5	2.5	88.2
3520B	3	341	10.0	9.7	54.0	25.8	3.7	4.6	46.9	2.1	2.1	86.7
3523V	4	352	11.9	10.5	52.3	24.4	4.8	5.7	54.1	2.0	2.6	77.8
3521V	4	362	11.6	10.8	51.1	26.5	4.6	5.3	48.7	2.1	2.2	93.8
3520V	4	366	10.9	10.7	49.3	27.9	4.6	4.9	46.2	2.1	2.5	83.3
3522V	4	381	11.3	10.6	51.4	26.5	4.5	5.5	51.9	1.8	2.4	77.8
3529V	4	386	10.6	10.0	52.9	27.5	3.8	5.2	51.9	2.1	2.3	88.9
MEAN		325.9	11.3	10.2	51.9	26.2	4.7	5.4	53.5	2.0	2.3	86.1

TABLE IV. Body proportions (in percentages) of males of *Lampetra fluviatilis*.

Tag No.	Stage of maturity	TL (mm.)	d-B ₁ TL	B ₁ -B ₂ TL	B ₂ -a TL	a-C TL	hD ₃ TL	d TL	d B ₁ -B ₂	O TL	O-B ₁ TL	O O-B ₁
3803B	0	108	11.1	8.3	52.8	24.1	3.2	4.6	55.5	2.8	2.8	100.0
3804B	0	109	12.9	8.7	49.5	27.5	3.7	5.5	63.2	2.8	2.8	100.0
3805B	0	114	11.9	7.9	51.8	25.4	3.5	5.3	66.7	3.1	2.6	120.0
2022DPQ	3	239	12.1	9.8	49.8	26.8	5.4	6.5	66.0	2.3	2.5	91.7
3964V	5	253	12.1	9.5	47.8	29.7	7.1	6.7	70.8	2.4	2.6	92.3
2014DPQ	3	255	12.2	9.6	50.8	26.7	5.1	5.3	55.1	2.4	2.6	92.3
3965V	5	264	12.5	10.2	46.2	29.4	7.2	6.6	64.8	2.3	2.7	85.7
6010B	3	265	11.3	9.6	52.1	25.3	—	4.9	51.0	1.9	2.5	76.9
6011B	3	266	10.7	9.6	51.5	28.2	6.0	5.3	54.9	1.9	2.4	76.9
2021DPQ	3	267	11.6	9.7	50.2	26.8	4.5	6.0	61.5	2.2	2.6	85.7
2018DPQ	3	273	11.7	9.2	50.9	26.9	5.0	5.3	58.0	2.2	2.6	85.7
2019DPQ	3	274	12.4	9.9	51.5	25.7	5.3	6.6	66.7	2.2	2.6	85.7
2009DPQ	3	281	11.2	9.3	51.9	26.2	4.5	5.3	57.7	2.1	2.5	85.7
2017DPQ	3	281	11.4	10.0	51.6	26.5	5.0	5.9	58.9	2.1	2.5	85.7
3966V	5	282	12.8	10.3	47.5	28.4	7.4	6.4	62.1	2.1	2.7	80.0
2001DPQ	3	283	11.1	9.5	51.9	28.3	—	5.7	59.3	1.8	2.5	85.7
3532V	4	290	12.4	10.7	49.7	26.7	5.2	5.9	54.8	2.3	2.4	92.9
3545V	4	292	12.0	10.3	51.0	26.7	6.5	6.3	59.7	2.1	2.4	93.8
3546V	5	296	12.8	10.5	48.1	29.1	7.8	6.6	62.9	2.5	2.5	100.0
3967V	5	297	12.1	10.1	46.5	30.3	6.1	6.1	60.0	2.0	2.5	80.0
3535V	4	298	12.1	10.7	51.2	26.8	4.7	5.7	53.1	2.0	2.5	80.0
3528V	3	305	11.8	9.8	50.9	27.9	4.8	5.1	51.7	2.3	2.5	93.3
3542V	4	308	11.5	9.6	51.3	26.9	5.8	6.2	57.5	1.9	2.3	93.3
3539V	4	314	12.4	10.2	50.6	26.6	4.8	6.1	59.4	2.4	2.6	93.8
3534V	4	338	11.2	9.8	51.8	26.3	4.1	5.6	57.6	2.1	2.3	87.5
3527V	4	350	11.6	9.7	52.0	26.9	4.4	5.4	55.9	2.2	2.4	88.2
3525V	4	352	11.5	10.5	52.1	26.0	4.4	5.4	55.9	1.9	2.4	88.2
3530V	4	360	11.1	10.8	53.6	25.8	4.2	4.7	43.6	2.2	2.4	94.1
3533V	4	362	11.1	9.3	52.5	26.8	5.0	5.5	59.7	2.2	2.4	94.1
MEAN		263.6	11.8	9.8	50.5	27.1	5.3	5.7	58.7	2.3	2.5	90.2

TABLE V. Average body proportions of transformed specimens of *Lampetra ayresii* and *Lampetra fluviatilis* (from Tables I—IV).

Species	Sex	Number of specimens	TL (mm.)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$	$\frac{hD_2}{TL}$	$\frac{d}{TL}$	$\frac{d}{B_1-B_7}$	$\frac{O}{TL}$	$\frac{O-B_1}{O-B_1}$
<i>L. ayresii</i>	♀	35	167.7	12.4	9.0	48.6	27.0	3.7	5.6	61.9	3.3	146.2
<i>L. fluviatilis</i>	♀	19	325.9	11.3	10.2	51.9	26.2	4.7	5.4	53.5	2.0	86.1
<i>L. ayresii</i>	♂	33	164.7	12.6	9.0	49.5	27.3	3.5	5.7	64.2	3.2	143.3
<i>L. fluviatilis</i>	♂	29	263.6	11.8	9.8	50.5	27.1	5.2	5.7	58.7	2.3	90.2

TABLE VI. Number of trunk myomeres in *Lampetra ayresii*. Specimen No. 3819B is the neotype. (a = ammocoetes; t = transformed individuals.)

Geographical region	Locality	Date	Tag. No.	TL (mm.)	Stage	Number of specimens	Number of myomeres											Mean	
							60	61	62	63	64	65	66	67	68	69	70		71
British Columbia	Skeena River	July 16, 1955	2622V	163	t	1	—	—	—	—	—	—	—	1	—	—	—	—	66.0
	Lake Sammamish Puyallup River	Oct. 12, 1949 June 22, 1940	3548V 4584R	311 158	t t	1 1	—	—	—	—	—	—	—	—	1	—	—	—	67.0 60.0
Oregon	Columbia River (Bonneville)	March 1940	1320B	281	t	1	—	—	—	—	—	—	—	—	1	—	—	—	67.0
	Yaquina	Nov. 14, 1949	1321B	211	t	1	—	—	—	—	1	—	—	—	—	—	—	—	64.0
California	Mill Creek do.	1954-1955 do.	1526J-1530J 1523J-1525J	109-151 197-205	a t	5 3	—	—	—	—	—	—	—	2	—	1	2	—	67.6 66.7
	Sacramento River (Meridian)	Apr. 29, 1954	4408R	102	a	1	—	—	—	—	—	1	—	—	—	—	—	—	65.0
	do.	do.	4400R-4407R	168-236	t	8	—	—	—	—	—	—	1	—	1	4	2	—	68.7
	Sacramento River (Cache Slough)	Jan. 20, 1954	947B	146	a	1	—	—	—	—	—	1	—	—	—	—	—	—	65.0
	Sacramento River (Isleton)	Jan. 14-Feb. 15, 1949	729V 3968V-3972V	146-172 152-158	a a	6 2	—	—	—	—	—	1	5	—	—	—	—	—	65.8 66.0
	Sacramento River (Isleton)	Mar. 17, 1947- Feb. 25, 1949	702V-728V 3955V-3963V	117-183	t	36	—	—	—	—	—	—	2	6	5	10	10	3	68.8
	Sacramento River (Rio Vista)	Nov. 4, 1946- Feb. 3, 1949	3990R-3999R	128-220	t	10	—	—	—	—	—	—	2	2	4	2	—	—	67.6
	Middle River (near Mossdale)	May 5, 1948	1500J-1503J	143-161	a	4	—	—	—	—	—	—	—	—	1	1	1	1	68.5
	San Joaquin River	Mar. 18-Apr. 22, 1947	1505J-1506J	120-123	t	2	—	—	—	—	—	—	—	—	—	1	1	—	68.5
	Delta-Mendota Canal	Jan. 29-Feb. 19, 1947	1507J-1509J	146-204	t	3	—	—	—	—	—	—	—	1	2	—	—	—	66.7
	San Francisco Bay (Pacific Gas and Electric Co. intake)	Dec. 24, 1945	4615R	213	t	1	—	—	—	—	—	—	—	—	1	—	—	—	67.0
	San Francisco Bay (Point Richmond)	Feb. 7, 1954	3819B (neotype)	147	t	1	—	—	—	1	—	—	—	—	—	—	—	—	63.0
TOTAL					a	19	—	—	—	—	—	4	7	2	2	3	1	—	66.8
					t	69	1	—	—	1	1	—	8	15	17	12	3	—	68.0

TABLE VII. Number of trunk myomeres in *Lampetra fluviatilis*. (a = ammocoetes; t = transformed individuals.)

Geographical region	Date	Tag No.	TL (mm.)	Stage	Number of myomeres											
					Number of specimens		58	59	60	61	62	63	64	65	66	Mean
Sweden	July 1955	3825B-3831B}	46-130	a	8	2	2	—	2	3	—	1	—	—	—	60.3
	1955	3623V}	273-278	t	2	—	—	—	—	—	1	—	1	—	—	63.0
U.S.S.R.	May 30, 1930	3874B-3879B}	65-116	a	6	—	—	—	1	2	—	2	1	—	—	62.0
	Sept. 1948	3870B-3873B}	265-332	t	7	—	—	—	—	1	3	2	1	—	—	62.4
Poland	May 27, 1956	927B-946B}	80-145	a	17	3	4	4	4	6	—	—	—	—	—	59.8
Czechoslovakia	1947	2011DPO}	123-341	t	3	—	—	—	—	—	1	1	1	—	—	63.0
		3820B-3821B}														
Netherlands	Nov. 1949	3520V-3539V}	290-386	t	20	—	—	—	—	—	1	2	5	8	4	64.6
Belgium	Apr. 30, 1955	3540V-3546V}	276-318	t	6	—	—	—	—	—	—	3	1	2	—	63.8
England	Mar. 1952	3816B-3818B}	56-104	a	3	—	—	—	—	1	2	—	—	—	—	61.7
	Mar. 1952	3803B-3805B}														
	Apr. 5, 1954	3964V-3967V}	108-309	t	23	—	—	—	—	6	3	9	4	1	—	62.6
	Nov. 1951	1409J-1424J}														
TOTAL				a	34	5	4	4	7	12	2	3	1	—	—	60.4
				t	61	—	—	—	—	7	9	17	13	11	4	63.4

TABLE VIII. Number of trunk myomeres in *Lampetra ayresii* and *Lampetra fluviatilis*. (a = ammocoetes; t = transformed individuals.)

Geographical Region	Species	Stage	Number of specimens	Number of myomeres													Mean			
				58	59	60	61	62	63	64	65	66	67	68	69	70		71		
Western North America	<i>L. ayresii</i>	a	19	—	—	—	—	—	—	—	—	—	4	7	2	2	3	1	—	66.8
		t	69	—	—	1	—	—	1	1	—	8	15	11	17	12	3	—	68.0	
Europe	<i>L. fluviatilis</i>	a	34	5	4	7	12	2	3	1	—	—	—	—	—	—	—	—	60.4	
		t	61	—	—	7	9	17	13	11	4	—	—	—	—	—	—	—	63.4	

TABLE IX. Number of cusps on the infraoral lamina and transverse lingual lamina in *Lampetra ayresii* and *Lampetra fluviatilis*.

Geographical Region	Number of specimens	Infraoral cusps					Number of specimens	Transverse lingual cusps									
		7	8	9	10	Mean		11	12	13	14	15	16	17	Mean		
Western North America	65	3	1	59	2	8.9	<i>Lampetra ayresii</i> 13	—	1	3	3	4	1	1	14.3		
Sweden	2	—	—	2	—	9.0	<i>Lampetra fluviatilis</i> 2	1	1	—	—	—	—	—	11.5		
U.S.S.R.	7	4	—	3	—	7.9	—	—	—	—	—	—	—	—	—		
Czechoslovakia	3	—	—	3	—	9.0	2	—	1	—	—	1	—	—	13.5		
Netherlands	18	11	1	6	—	7.7	15	—	2	4	2	6	1	—	14.0		
Belgium	7	5	—	2	—	7.6	1	—	—	—	1	—	—	—	14.0		
England	22	4	1	17	—	8.6	17	4	2	7	1	3	—	—	12.8		
TOTAL FOR EUROPE	59	24	2	33	—	8.2	37	5	6	11	4	10	1	—	13.3		

TABLE X. Number of cusps on the longitudinal lingual laminae in *Lampetra ayresii* and *Lampetra fluviatilis*.

<i>Lampetra ayresii</i>				<i>Lampetra fluviatilis</i>			
Tag. No.	Left	Right	Total	Tag No.	Left	Right	Total
701V	10	9	19	2017DPQ	10	9	19
4407R	9	11	20	3611V	10	10	20
1506J	10	10	20	2009DPQ	11	11	22
3819B	11	10	21	3821B	12	11	23
1507J	10	12	22	2001DPQ	11	12	23
4615R	11	11	22	2015DPQ	12	12	24
				2033DPQ	13	13	26
MEAN	10.2	10.5	20.7	MEAN	11.3	11.1	22.4

TABLE XI. Variation in the degree of pigmentation on the tail and on parts of the head of larger ammocoetes (TL 100 mm. or more) of *Lampetra ayresii* and *Lampetra fluviatilis*. (— = absence of pigmentation; + = weak pigmentation; ++ = moderate pigmentation.)

Geographical Region	Number of specimens	Tail		Upper lip		Subocular region			Postorbital region			Prebranchial blotch			Branchial region	
		—	+	++	—	+	++	—	—	+	—	+	++	—	—	+
California	12	—	—	12	12	12	—	—	<i>Lampetra ayresii</i>			—	—	—	12	—
	%	—	—	100	100	100	—	—	—	—	—	—	—	—	100	—
Sweden U.S.S.R. Poland England	1	1	—	—	—	—	—	—	<i>Lampetra fluviatilis</i>			—	—	—	1	—
	4	4	—	—	4	—	—	—	—	1	3	1	1	—	4	—
	14	14	—	—	14	—	—	—	—	13	1	9	5	—	14	—
	1	1	—	—	1	—	—	—	—	1	—	—	—	—	1	—
TOTAL FOR EUROPE	20	20	—	—	20	—	—	—	—	16	4	11	9	18	1	20
	%	100	—	—	100	—	—	—	—	80	20	55	45	90	5	100

TABLE XII. Body proportions (in percentages of total length) of ammocoetes of *Lampetra ayresii*.

Tag No.	TL (mm.)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$
4408R	102	8.3	11.8	52.0	26.5
1502J	143	6.6	10.5	51.7	26.6
947B	146	6.9	10.3	54.8	27.1
1503J	146	6.8	11.0	51.4	26.7
3970V	146	7.2	10.6	54.1	27.4
3971V	147	6.5	10.9	52.4	27.6
1501J	150	6.7	10.0	54.7	26.7
3972V	153	6.9	10.5	52.9	28.9
729V	157	6.4	10.5	53.5	27.4
1500J	161	5.9	9.9	54.7	27.3
3969V	171	6.1	9.6	55.0	27.5
3968V	172	6.4	9.9	54.1	27.3
MEAN	150.0	6.7	10.5	53.4	27.3

TABLE XIII. Body proportions (in percentages of total length) of ammocoetes of *Lampetra fluviatilis*.

Tag No.	TL (mm.)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$
943B	100	8.0	13.0	52.0	26.0
939B	100	8.5	12.5	51.5	26.0
3877B	101	7.9	12.4	52.0	26.2
3826B	103	8.3	12.1	50.0	27.7
940B	105	8.6	12.9	51.0	25.7
3876B	106	8.5	12.7	50.9	26.4
938B	112	8.9	11.2	51.3	26.8
3875B	115	7.8	11.7	50.9	27.4
3874B	116	7.8	12.1	51.7	25.9
930B	116	7.8	12.1	49.1	28.5
932B	117	6.8	12.4	52.1	26.5
937B	117	7.7	12.0	51.3	27.4
935B	118	9.3	12.7	50.4	25.4
931B	121	8.3	13.2	51.2	25.6
932B	122	8.2	12.3	51.6	26.2
936B	123	8.3	12.5	53.8	25.8
934B	131	7.6	12.2	52.7	25.2
929B	140	7.2	11.8	53.6	25.7
927B	144	7.6	11.1	53.5	25.7
928B	145	7.6	11.7	53.1	25.5
MEAN	117.6	8.0	12.2	51.7	26.3

TABLE XIV. Body proportions (in percentages of total length) of ammocoetes of *Lampetra ayresii* and *Lampetra fluviatilis*. (Minimum, maximum, and (in italics) average values.)

Species	TL (mm.)	Number of specimens	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$
<i>L. ayresii</i>	102-172 <i>150.0</i>	12	5.9-8.3 <i>6.7</i>	9.6-11.8 <i>10.5</i>	51.7-55.0 <i>53.4</i>	26.5-28.9 <i>27.3</i>
<i>L. fluviatilis</i>	100-145 <i>117.6</i>	20	6.8-9.3 <i>8.0</i>	11.1-13.2 <i>12.2</i>	49.0-53.8 <i>51.7</i>	25.2-28.5 <i>26.3</i>

Circulation on the Scotian Shelf as Indicated by Drift Bottles^{1,2}

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ABSTRACT

The surface circulation on the Scotian Shelf has been investigated by means of 827 drift bottles released by the Naval Research Establishment in August, 1954. The study suggests a cyclonic circulation centred in the vicinity of Sable Island Bank but with the eastern part incompletely determined by the results. Calculated speed of drift varies from 0.11 to 0.15 knot.

INTRODUCTION

THE SYSTEMATIC STUDY of the oceanography of the Scotian Shelf started with the Canadian Fisheries Expedition of 1914-15 (Bjerkas, 1919), was continued from then through 1937 by the Biological Board of Canada, and since 1938 by that Board under its new name, the Fisheries Research Board of Canada.

Apart from the Board's releases of drift bottles from 1922 to 1926 (not published; see Bigelow, 1924, p. 908), most of the observations have been of temperature and salinity. These have permitted descriptive studies of the water masses (Hachey, 1937, 1942; McLellan and Trites, 1951; McLellan, 1954), as well as calculations of geostrophic current patterns and volume transports (Hachey, 1938, 1947). The reliability of the results of the dynamic considerations depends upon the degree to which the necessary simplifying assumptions are valid. In an area such as the Scotian Shelf where the depth is so variable and the validity of the steady state assumption is questionable, there is a strong need for direct current measurements supplementing the other oceanographic observations if the circulation pattern is to be determined with confidence. It was this fact that prompted the drift bottle releases reported herein. It was hoped that from this preliminary experiment certain pertinent features would be revealed indicating where further direct current measurements should be concentrated.

DRIFT BOTTLE METHOD

Sealed bottles (Fig. 1) ballasted with sand and fitted with drags to minimize the direct effect of wind, each containing an explanatory leaflet and a numbered post card questionnaire, were released at a network of stations covering the area under study.

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²Published with permission of the Defence Research Board of Canada.

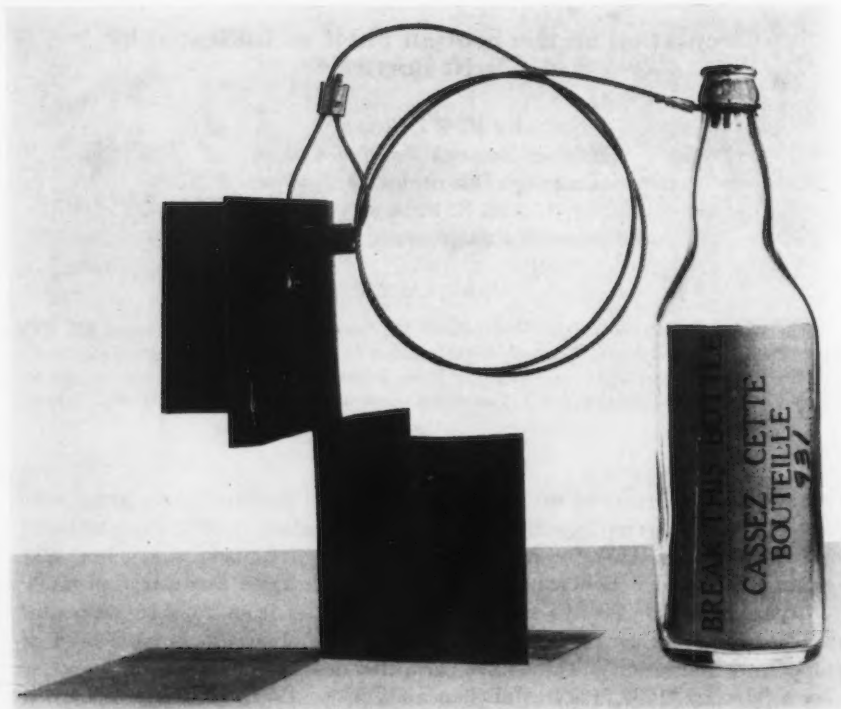


FIG. 1. Drift bottle.

The success of the drift bottle method depends upon the number of cards returned with information concerning the position and time of recovery. Since usually only a small percentage of the cards are returned, this necessitates the use of large numbers of bottles, particularly where adjacent coasts are thinly populated. However, despite this limitation, the method has been used with some success in such scantily populated areas as around certain parts of Hudson Bay (Hachey, 1935).

Interpretation of the results of drift bottle experiments must be undertaken with care. Positive conclusions cannot be drawn from the lack of returns, especially where sparsely populated coasts are involved. Indications of the speed of drift are usually doubtful except for returns from normally frequented beaches or bottles retrieved at sea. Bottles travelling along the coast may have their drift interrupted from time to time as eddying currents carry them into shallow water.

Despite these limitations, the probable paths of drift can be determined by considering the points at which the bottles were released and recovered in conjunction with wind and horizontal sea temperature and salinity patterns.

THE EXPERIMENT

During the period August 11-17, 1954, a total of 827 bottles was released in groups of five or ten at 10-mile intervals along four lines running out from the coast of Nova Scotia and in a more closely spaced network immediately off Halifax (see Fig. 2). Throughout the cruise, bathythermographic observations were taken at 5-mile intervals and water samples collected at serial depths approximately every 20 miles by means of a Sea Sampler.

By mid-1956, 9.7% of the cards had been returned. A summary of these returns is given in the accompanying Table. In Fig. 2, the release positions are shown for those bottles picked up on Sable Island and those that crossed the Atlantic Ocean.

Area	No. of bottles released	Percentage returned	Number of bottles returned, by area			Drags attached		
			Sable Island	Europe and Azores	Nova Scotia	Yes	No	No reply
Vicinity Halifax	270	14	24	2	8 (ashore) 4 (at sea)	12	17	9
Line I	110	5	4	1	1 (at sea)	3	2	1
Line II	117	8	7	2	Nil	1	5	3
Line III	140	12	15	2	Nil	6	2	9
Line IV	190	5	6	4	Nil	2	3	5
All areas	827	9.7	56	11	13	24	29	27

Of the bottles returned, two-thirds have come from Sable Island. The others (3% of those released) were returned from the south and western shores of Nova Scotia, one from the Bay of Fundy and eleven from the eastern side of the Atlantic, including from the Azores, Ireland, Scotland, Shetland Islands, France and Norway. Only two bottles were returned from that section of the Nova Scotia coast east of Halifax. There were no returns from Cape Breton, from Maine, or any other point along the United States seaboard.

DISTRIBUTION OF PROPERTIES

An examination of the horizontal sea temperature and salinity patterns suggests possible circulation patterns that assist in the interpretation of the bottle returns.

Plots of the mean temperature and salinity of the surface layer are shown for the periods August 11-18, 1954, in Fig. 3 and 4; August 18-28, 1954, in Fig. 5 and 6; and for October 8-31, 1954, in Fig. 7 and 8. The plots for the two later periods are based on data provided by the Fisheries Research Board of Canada's Atlantic Oceanographic Group. All these plots show the same general features. The isopleths near the coast are approximately parallel to it, suggesting flow parallel to the coast. Similarly, beyond the continental shelf the flow again parallels the coastline. In the area between these extremes the pattern is more complex and the horizontal gradients of temperature and salinity are smaller.

Although little is known of the intensity of the mixing process or of the transfer of heat across the air-sea boundary, it can be concluded that surface currents are likely small and variable over the large central part of the shelf.

Two other features are of interest. The southerly flow around the Cape Breton coast (Bigelow, 1924; Huntsman *et al.*, 1954; MacGregor, 1956) is indicated by the distribution of salinity, particularly in Fig. 6. The presence of low temperatures at the southern tip of Nova Scotia in the region of Cape Sable is evident in each of the three periods, although less marked in October. This apparently permanent feature of the area is undoubtedly due to sub-surface water reaching the surface by either vigorous tidal mixing or by a horizontally divergent flow, with a compensating upwelling of deeper water.

SURFACE CIRCULATION

Considering the locations of the bottles recovered relative to their release positions and using the temperature and salinity plots as rough guides, the pathlines for the surface flow have been sketched in Fig. 9. This pattern illustrates the net flow averaged over several months and consequently appears as a much simpler pattern than would be indicated if flow lines were plotted for weekly or fortnightly averages.

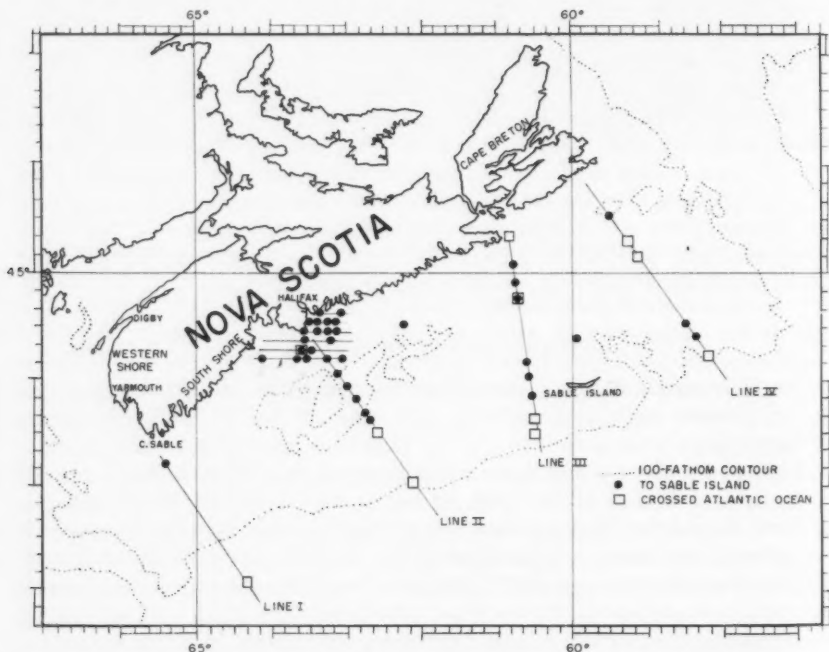


FIG. 2. Chart showing lines along which bottles were released, together with positions for these bottles that drifted ashore on Sable Island or crossed the Atlantic Ocean.

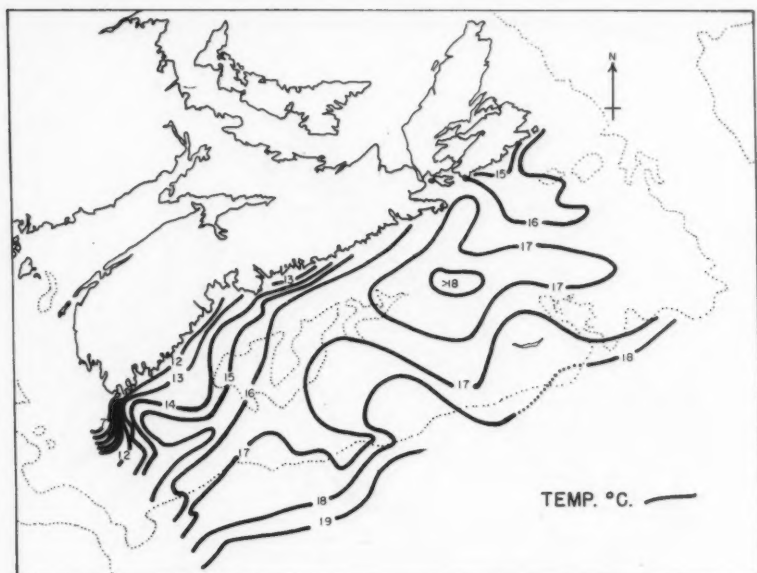


FIG. 3. Mean temperature (°C.) of surface layer, August 11-18, 1954.

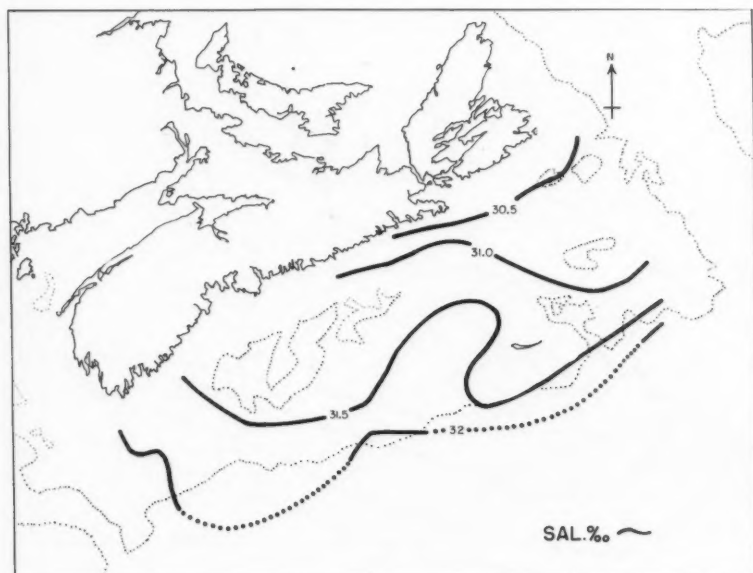


FIG. 4. Mean salinity (‰) of surface layer, August 11-18, 1954.

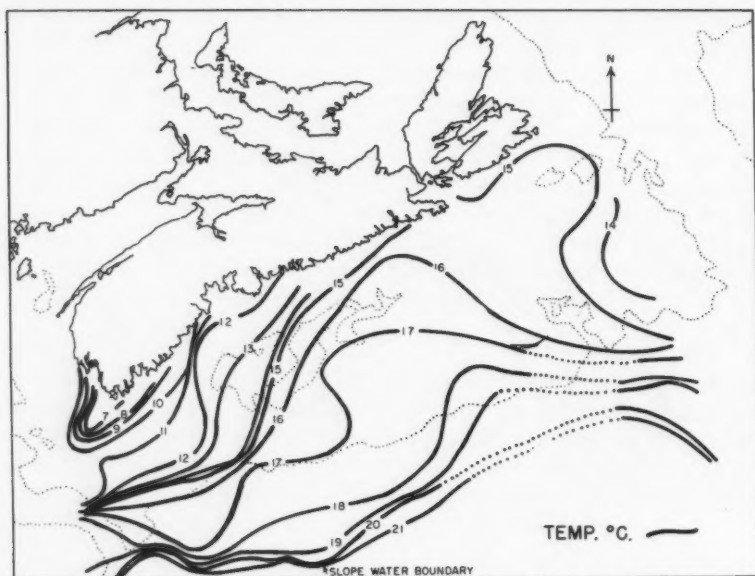


FIG. 5. Mean temperature (°C.) of surface layer, August 18-28, 1954.

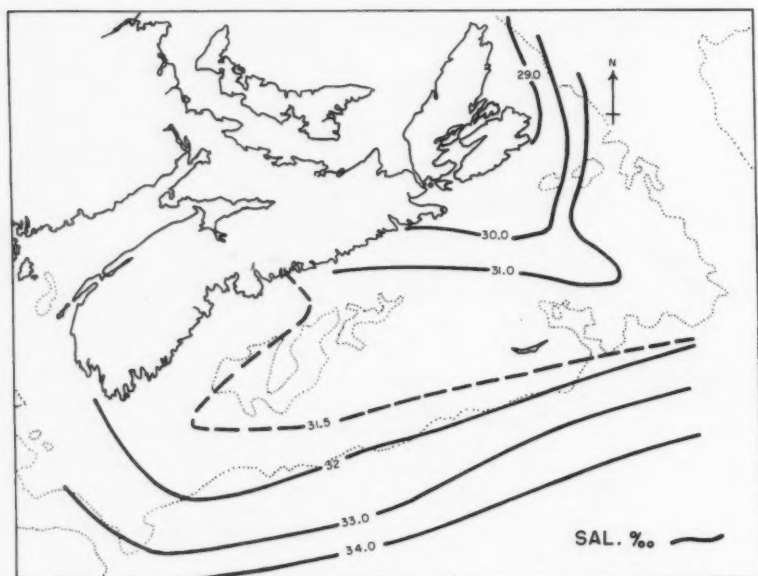


FIG. 6. Mean salinity (‰) of surface layer, August 18-28, 1954.

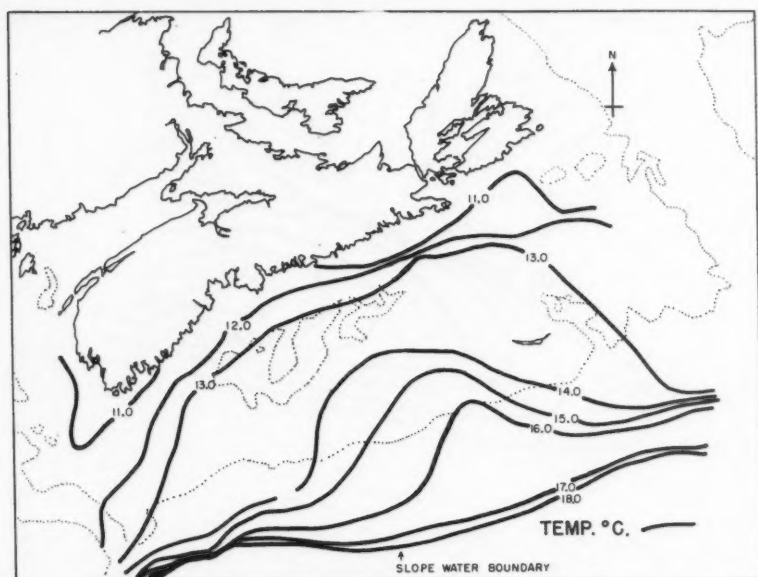


FIG. 7. Mean temperature ($^{\circ}\text{C}.$) of surface layer, October 8-31, 1954.

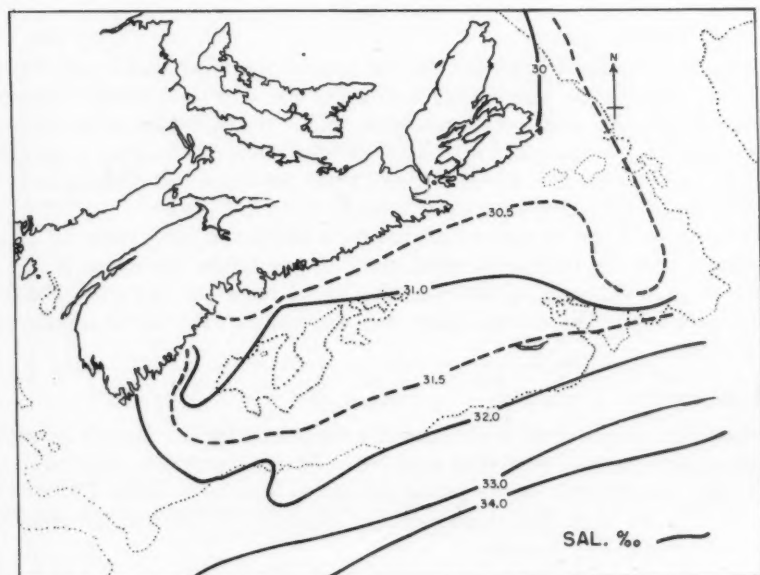


FIG. 8. Mean salinity (‰) of surface layer, October 8-31, 1954.

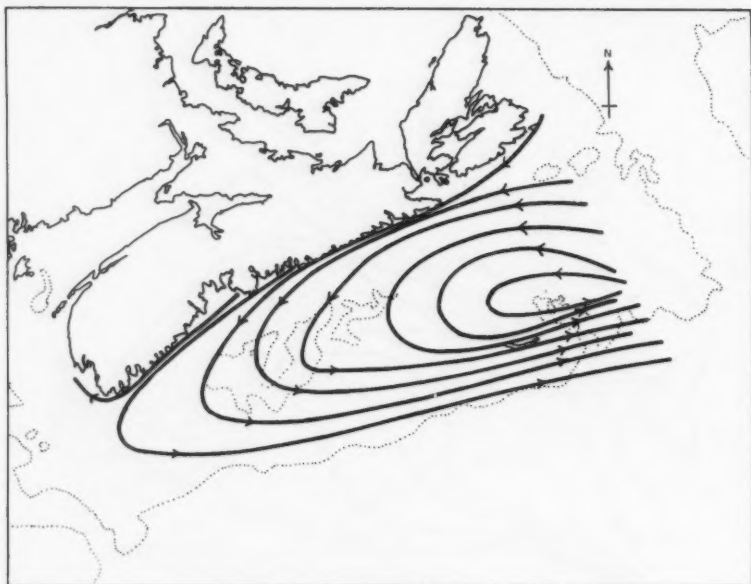


FIG. 9. Net surface circulation pattern for period August–November, 1954, as deduced from drift bottle and distribution of properties.

SPEED OF DRIFT

The highest speed indicated by the returns from the south and western shores of Nova Scotia was 3 (nautical) miles per day (0.12 knot). However, one bottle released south of Cape Sable, N.S., travelled 250 miles to Sable Island with an average speed of 8 miles per day (0.33 knot). This is probably much higher than the surface layer speed, since the bottle lost its drag en route and therefore would have been more influenced by the wind.

Average drift speeds were calculated for a number of cards returned on the assumption that the bottles travelled along the pathlines illustrated in Fig. 9. Nearly all gave values lying between 2.7 and 3.7 miles per day (0.11 and 0.15 knot respectively). The lowest values were generally in the southwesterly flow near the coast.

WIND ANALYSIS

Since the surface drift is considerably influenced by the prevailing winds, an analysis was made of wind data from Sable Island, Yarmouth, and the Naval Air Station, Dartmouth, for the period August to November, 1954. The results, given in Fig. 10, show the magnitude and direction of the average resultant wind vector for 15-day periods.

Sable Island, with its low topography and offshore position, would be expected to give the most representative wind data for the Scotian Shelf. However,

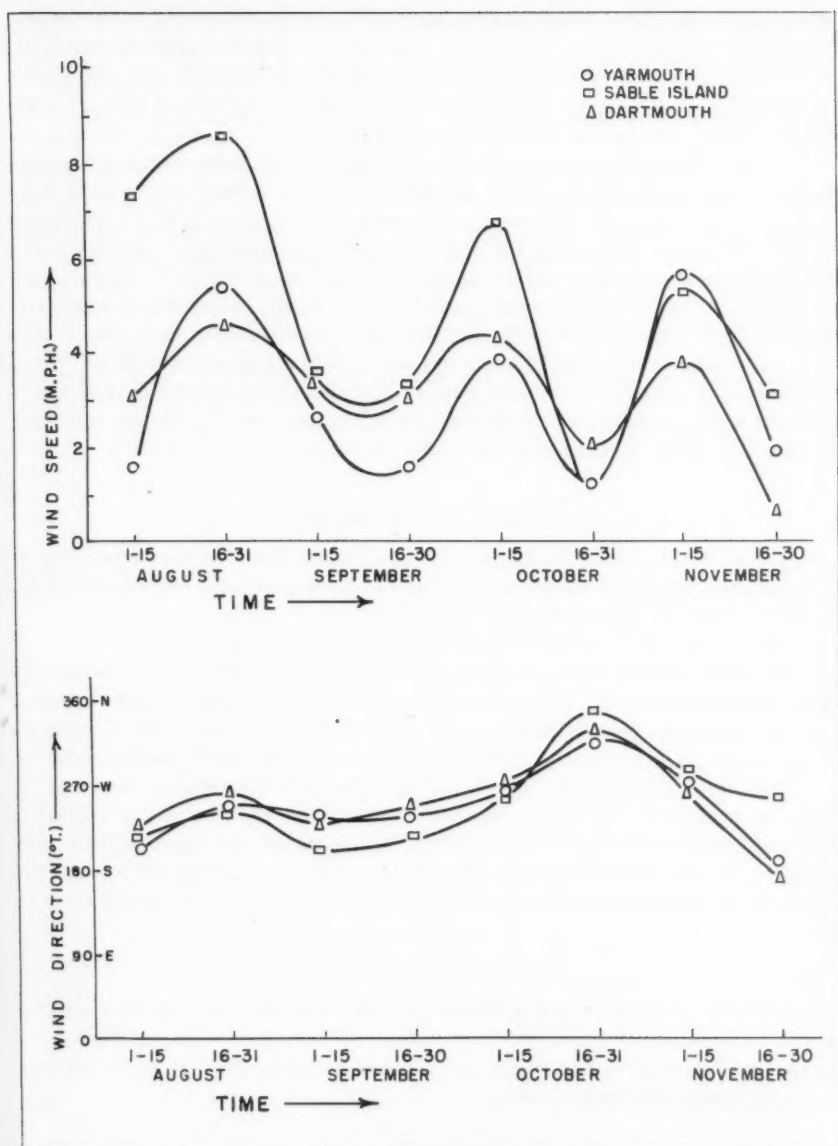


FIG. 10. Average magnitude and direction of the wind for 15-day intervals, August–November, 1954, at three stations around the Scotian Shelf.

the analysis reveals a remarkable uniformity in wind direction and in the relative variation of speed from one period to the next at all three stations, but shows a considerable spread in the absolute magnitude of wind speeds in any one period. In general, the wind speed is lower at Dartmouth and Yarmouth than at Sable Island, which may be due to their mainland positions.

During the entire period, the resultant wind was predominantly westerly at 1.2 to 8.3 m.p.h. For half the period the resultant wind was greater than 5 m.p.h. Thus it appears that the surface flow near the coast was directed opposite to the wind stress. This indicates that in this area, other forces, possibly density differences, exert a greater effect on the flow than does the wind. Hachey and Fothergill (1953), who made an analysis of the winds and surface currents at Sambro Light Vessel, likewise found that under certain conditions the surface flow was directed opposite to the wind stress. They concluded that for winds in excess of 10 m.p.h. the surface current, both in direction and magnitude, is strongly influenced by the wind force and direction, but for speeds less than 10 m.p.h. no such correlation exists.

SUMMARY AND CONCLUSION

A net surface circulation pattern for the Scotian Shelf for the period August to November, 1954, has been presented on the basis of returns from drift bottles released during the period August 11-17, 1954.

The average speed of flow varied from 0.11 to 0.15 knot.

The large number of returns from Sable Island (see Table) cannot be entirely explained by the ideal conditions for recovery on its gently sloping sandy beaches. The movement of these bottles from all areas of release to Sable Island suggests the presence of a large cyclonic eddy centered in the vicinity of Sable Island Bank.

The results, obtained during about four months of a particular year, cannot claim to represent average conditions. Indeed the distribution of physical properties observed at different seasons of a number of years gives evidence of variation in flow depending upon season. Further direct observations are required to establish completely the circulation pattern on the Scotian Shelf.

ACKNOWLEDGMENTS

The authors wish to acknowledge the use of wind observations compiled by the Meteorological Division, Department of Transport, Canada. Particular thanks are extended to the many people who, by searching out and returning the cards, made this study possible.

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Sea Water Intrusion into the Fraser River and its Relation to the Incidence of Shipworms in Steveston Cannery Basin¹

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ABSTRACT

The presence of shipworms (*Bankia setacea*) in Steveston Cannery Basin in the Fraser River estuary is attributed to sea water intrusion. River discharge, tides, geometry of the river channel and basin, and density of the intruding sea water are factors affecting intrusion, which in turn influence larval settlement. Settlement may occur at depths where salinity is less than 15‰ but the larvae fail to survive. However, they will continue to develop where salinity exceeds 20‰. Dredging the channel to a continuous grade would eliminate permanent salt-water "pools" along the bottom and prevent infestation.

INTRODUCTION

THE ESTUARY AND APPROACHES to the Fraser River (Fig. 1) constitute one of the principal salmon fishing areas on the Pacific Coast. Most of the fishing vessels in this area operate from the town of Steveston, about 6 nautical miles³ upstream from the river mouth. This harbour is located in Steveston Cannery Channel which is separated from the main river channel by Steveston Island. The 2 miles of waterfront are crowded with wharves and canneries, most of which rest on untreated wooden pilings.

In order to provide a protected harbour for the shipping (Fig. 2) the Harbours and Rivers Engineering Branch of the Department of Public Works of Canada constructed a rock dam across the upstream end of the Cannery Channel, and a rock breakwater along the shoal from the western end of Steveston Island to within several hundred feet of Garry Point. This was completed in 1954 when the channel became a tidal basin with an outlet at the downstream end.

The closure of the channel aroused fears that there might be a prolonged sea water intrusion in the basin, making it a suitable habitat for shipworms, and exposing the pilings to infestation and possible destruction.

To determine if these fears were justified, co-ordinated oceanographic and biological investigations were undertaken by the Pacific Oceanographic Group and the Biological Station (Nanaimo, B.C.) of the Fisheries Research Board of Canada, and the Department of Public Works of Canada.

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²Pacific Oceanographic Group.

³Note: for conversion to metric units the following may be used:

1 nautical mile	= 1.853 kilometers	1 cubic foot	= 0.0283 cubic meter
1 knot	= 1.853 kilometers per hour	1 inch	= 25.4 mm.
1 foot	= 0.305 meter	1 square inch	= 6.54 square cm.
1 square foot	= 929.0 square cm.		

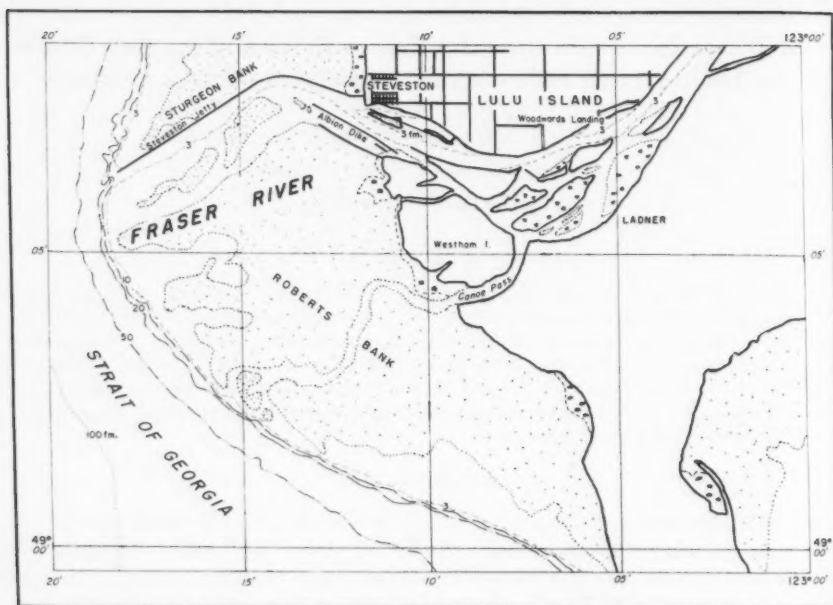


FIGURE 1. Chart showing location of Steveston and adjacent waters.

These investigations showed that sea water intruded the basin except during the summer freshet period; that sea water remained in the depression in the basin throughout the year; and because of these conditions shipworm infestations can and do occur in some of the wharf pilings.

GEOGRAPHY OF THE REGION

The main channel of the south arm of the Fraser River lies between two intertidal banks, Sturgeon Bank on the northern side and Roberts Bank on the southern side (Fig. 1). These banks of alluvial mud and sand extend from the land seaward for about 5 nautical miles. There the bottom rapidly increases in depth to about 300 feet within a quarter of a mile off the low tide boundary. The channel is protected on the northern side by Steveston Jetty that extends for about 5 nautical miles to seaward, and to a lesser extent by the Albion Dyke on the southern side. It has an irregular bottom with depths ranging from 20 to 40 feet⁴ along most of its course. A secondary channel, Canoe Pass, cuts through Roberts Bank but is much shallower (minimum depth of 3 feet) than the main channel.

⁴The elevation of sea level referred to in this study is based on the Public Works datum at Sand Heads which is 8.54 feet below the Geodetic Survey of Canada datum (1951) and is 1.3 feet above the Point Atkinson datum of the Canadian Hydrographic Service.

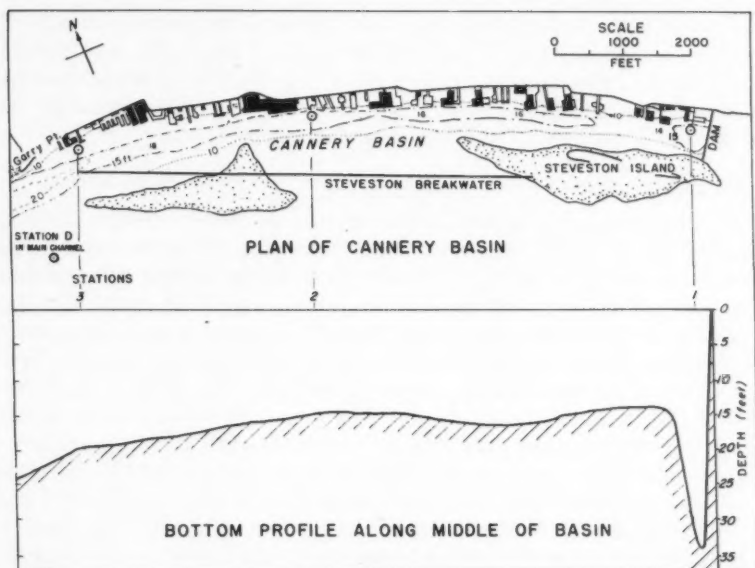


FIGURE 2. Chart showing Steveston Cannery Basin, bottom profile along its middle section, and station positions.

Steveston Cannery Basin is about 9,000 feet long, about 1,000 feet wide, and has depths generally between 15 and 20 feet (Fig. 2). There are two depressions below the general grade of the bottom, one just seaward of the basin (see Fig. 3b) and another at the head (Fig. 2). The latter has a depth of 34 feet which is about twice that of the general grade.

TIDES

The tides in this region are of the semi-diurnal mixed type having two high waters and two low waters daily. Their diurnal inequality is least when the moon is on the Equator (Equatorial Tides) and largest when the moon is at maximum declination (Tropic Tides). The Equatorial Tides occur twice a month for two short periods and are almost equal in height with a range from 5 to 13 feet above the Public Works datum. An example is shown later in Figure 8(a). The Tropic Tides occurring between these periods have much larger diurnal inequality in the successive low waters than in the high waters of the same day. The lesser of the twice-daily tides are known as half tides. During these Tropic Tides the diurnal range may approach a maximum of 17 feet, and the low waters fall to the datum level. An example of these tides is shown later in Figure 7(a).

FRASER RIVER DISCHARGE

The discharge of the Fraser River varies from a minimum of about 30,000 cubic feet per second during the winter months (January-March) to a maximum

of ten times this volume during the freshet period in the summer months (June-July). It rises rapidly from about 100,000 c.f.s. in May to a peak toward the end of June, and then decreases more gradually to the lower levels in the autumn. The illustration shown later in Figure 9(b) indicates the discharge⁵ during 1954-55 and is typical of the Fraser River runoff.

OCEANOGRAPHIC OBSERVATIONS—WEEKLY OBSERVATIONS OF SALINITY

In order to examine the seasonal variation of sea water intrusion in the basin, a programme of weekly salinity observations was initiated, commencing in August 1954 and terminating in October 1955. Three stations were established (Fig. 2), one at the head near the dam (Station 1), one at the middle (Station 2), and another at the outlet of the basin (Station 3). Water samples were obtained with Fjarlie or Ekman sampling bottles from a depth of 2 feet above the bottom, and at 2/10 of the total depth above the bottom. The salinity (in parts per thousand, ‰) was determined by the Mohr method (silver nitrate titration) from August 1954 to June 1955. From June to October, 1955, the salinity was measured *in situ* by conductivity measurements with a Solu-Bridge (Model No. RB-188-1). This instrument, manufactured in the United States by Industrial Instruments Inc., has one feature not contained in other instruments of this kind. Its conductivity readings are automatically corrected for temperature differences of the sample, and thus the specific conductance, which can easily be converted into salinity, is read directly.

OCEANOGRAPHIC SURVEYS

Four oceanographic surveys were made in the main channel and in the basin to determine the mechanism of sea water intrusion, and the properties of this water. The details of the surveys are summarized in Table I.

DISTRIBUTION OF SALINITY

The distribution of salinity in the main river channel during the rising tide is shown in Figure 3(b). There were three layers of water: an upper layer of relatively fresh water (Fig. 3(b), 4(a)), a deep layer of sea water whose salinity was between 20‰ and 28‰, and an intermediate or boundary layer in which there was a marked salinity gradient between these two extremes.

The distribution of salinity in the basin during the rising tide (Fig. 5(a), 6(a)) was very similar to that in the main channel. The isohalines (20, 25‰, etc.) illustrated the extent to which sea water intruded the basin. During the falling tide the sea water began to withdraw seaward (Fig. 5(b)—note receding of the 26‰ isohaline) and shortly after low water (Fig. 5(c), 6(b)) it had almost completely retreated from the basin. This situation continued for a few hours and

⁵The discharge off Steveston was estimated by adding the volume of water from the tributaries in the 100 miles downstream from Hope, B.C., and subtracting 13% that leaves through the North Arm of the river (Parkinson, 1955). The flow through Canoe Pass is assumed to be negligible compared to that in the main channel.

TABLE I. Catalogue of the details of the surveys.

Survey No.	Dates	Vessels	Locations	Variables observed	Depths (<i>f</i> ₁) from which samples collected	Methods used	Remarks
I	7-10 Dec. 1954	C.N.A.V. <i>Ehkali</i> Royal Canadian Navy	Main river channel from the mouth to Steveston (Stations A, B, C—see Fig. 3)	Salinity Temperature Dissolved oxygen	0, 6, 9, 12, 15, 18, 21, 24, 27, 33 or as many as the depth allowed	Salinity: titration (Mohr method). Temperature: reversing thermometers, bathythermograph. Oxygen: titration (Winkler method)	All samples collected with Fjarlie or Ekman sampling bottles. More than 50 hours of bi-hourly observations made
II	19-20 April 1955	C.G.M.V. <i>Arifal</i> (Dept. of Public Works)	Basin (Stations 1, 2, 3—see Fig. 2)	Currents (At Station 3 only)	4 depths: 1 near surface. 2 above fresh-sea water boundary. 3 below fresh-sea water boundary 4 two feet above bottom	Ekman current meter	
		C.G.M.V. <i>Arifal</i>	One station in main river channel (Station D) and one station in basin (Station 3)	Salinity Temperature	0, 6, 9, 12, 15, 18, 21, 24, or as many as the depth allowed	Salinity: titration Temperature: reversing thermometers	All samples collected with Fjarlie or Ekman sampling bottles. 25 hours of bi-hourly observations made
III	25 April 1955	Same as above	Same as above	Same as above	Same as above	Same as above	Same as above, but 13 hours of observations
IV	9 May 1955	Same as above	Same as above	Same as above	Same as above	Same as above	Same as above

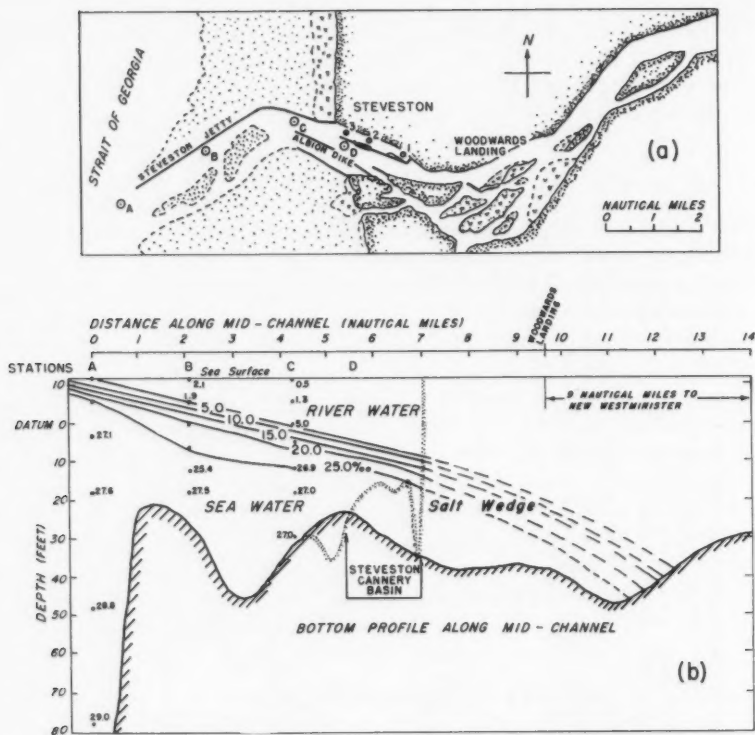


FIGURE 3. (a) Chart showing location of stations in the main channel of the Fraser River and in Steveston Cannery Basin.

(b) Vertical section of salinity along the length of the main channel during the rising tide (based on observations made between 1100 and 1300, 7 December 1954—see Figure 8 for tides at this period).

then, on the rising tide, the sea water flowed into the basin (Fig. 5(d)). During the half tides, the sea water remained in the basin.

The heights of the wharves in the basin are about 20 feet above the datum. Figures 7(a) and 8(a,b,c) indicate the intervals during which the different parts of the wharf pilings are exposed to water of various salinities. Above the datum, the water is relatively fresh for most of the time, but from this depth toward the bottom the salinity progressively increases to a maximum of 28‰.

TIDAL VARIATION OF SALINITY

Figure 7(a) shows the salinity of the basin water at Station 3 during tides of large range (December 1954). The range of the salinity of the surface water was less than 2‰, that of the intermediate water about 15‰, and of the bottom

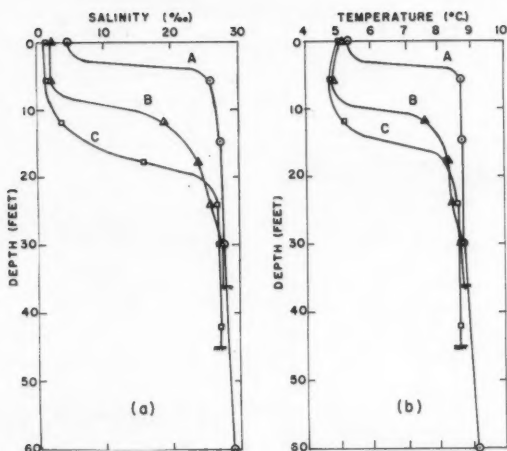


FIGURE 4. Salinity and temperature profiles at Stations A, B, and C in the main channel (December 6, 1954)

water more than 20‰. At all depths observed the salinity reached a minimum soon after low tide. A period of maximum salinity endured from about high tide, through the half tide, to a little after the second high tide.

At 5 feet above the datum (10 feet below the high water line) salinity greater than 5‰ seldom occurred. At zero datum salinity of 10‰ endured for about half a day, and at 10 feet below the datum (5 feet above the bottom) salinity of about 25‰ endured for more than half a day. Sea water of salinity greater than 25‰ remained along the bottom for more than three-quarters of a day. In contrast to this, the sea water was flushed from the main channel of the river (Station D) for a period of 6 hours (Fig. 8(b,c)).

The cycle of salinity structure observed in the basin in April 1955 (Fig. 8(b)) and May 1955 (Fig. 8(c)) was generally similar to that observed in the previous December. However the salinity at low tide was considerably greater, and the sea water was only partially flushed from the basin in April.

During tides of small range, when the two daily tides were of similar amplitude, the salinity in the basin fluctuated within a smaller range than during the large tides. At low tide there was an appreciable amount of sea water still left in the basin (Fig. 8(a)). As during the large tides, salinity greater than 5‰ seldom occurred at 5 feet above the datum. At zero datum salinity of 10‰ endured for less than one-quarter of a day and along the bottom, salinity greater than 25‰ endured throughout the tidal day. The main channel, on the other hand, was flushed for 2 hours (Fig. 8(a)).

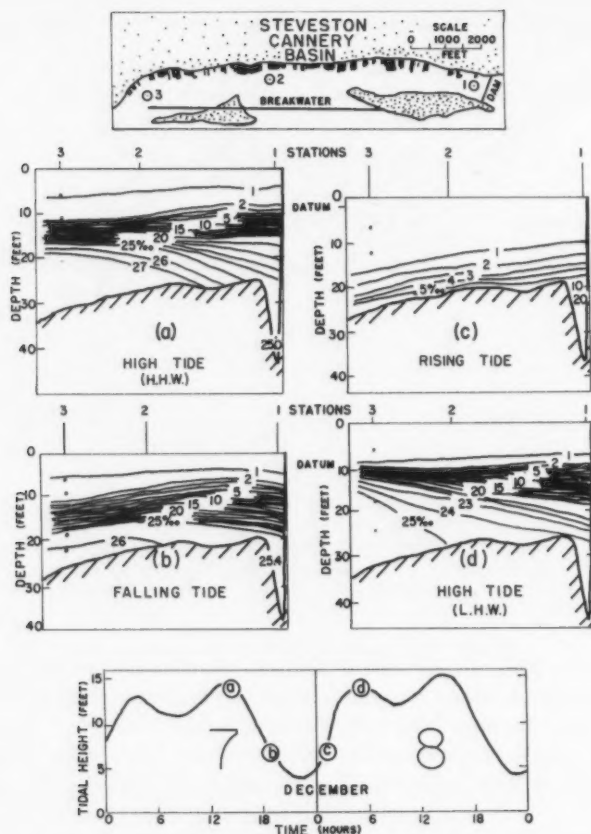


FIGURE 5. Distribution of salinity along the length of the Steveston Cannery Basin during the tidal stages:

- (a) High tide, (c) Rising tide,
(b) Falling tide, (d) High tide.

CURRENTS IN THE BASIN

Currents measured at depths of 3 feet and at 9 feet had similar velocities, the speed differing less than 0.2 knot with each other. They were also in phase with each other. Therefore they are combined and referred to as currents in the upper layer.

The currents (Fig. 7(b,c)) in the basin were of the reversing type and had periods similar to those of tides, though displaced in phase (compare with tides, Fig. 7(a)). At all depths measured they were of the same order of magnitude, generally less than 0.5 knot and reaching maximum strengths of 0.8 knot.

The maximum strengths of the currents in the upper layer occurred almost at the time of maximum rate of tidal rise (or fall) (Fig. 7(a,b)) and the slack

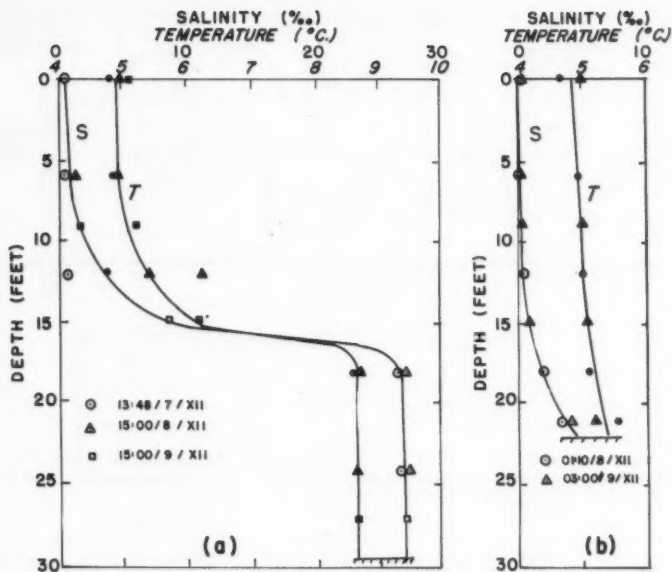


FIGURE 6. Representative salinity and temperature profiles at times of (a) maximum and (b) minimum sea water intrusion into Steveston Cannery Basin.

waters at times of tidal maxima and minima. The maximum strengths of the bottom currents, on the other hand, occurred almost at times of tidal maxima and minima and the slack waters at times of maximum rate of tidal rise (or fall). This cycle is therefore about 3 hours later than the current cycle in the upper layer.

MECHANISM OF SEA WATER INTRUSION

The elevation of the sea level caused by the rising tide in the Strait of Georgia imparts an upstream flow of dense sea water into the river. As it advances it lifts the lighter river water and carries it back upstream. This results in the flood current in the river channel. During river discharge of 50,000 c.f.s., the slope of the sea level caused by the rising tide is of the order of 2 : 100,000 in the river channel between Steveston and New Westminster, 13 nautical miles apart (calculated from data obtained by Baines, 1952). In the basin the current in the upper layer occurs in advance of the salt wedge (Fig. 5, 7).

The salinity distribution shown in Figure 3(b), in which the boundary layer slopes downward from the sea into the river, is known as a salt wedge. It illustrates the manner in which the sea water advances along the river channel and subsequently into the basin during the rising tide (Fig. 5(a)). This type of salt wedge is similar to that observed in the Savannah River in Georgia and the Cooper River in South Carolina (Rhodes, 1950; Simmons, 1952).

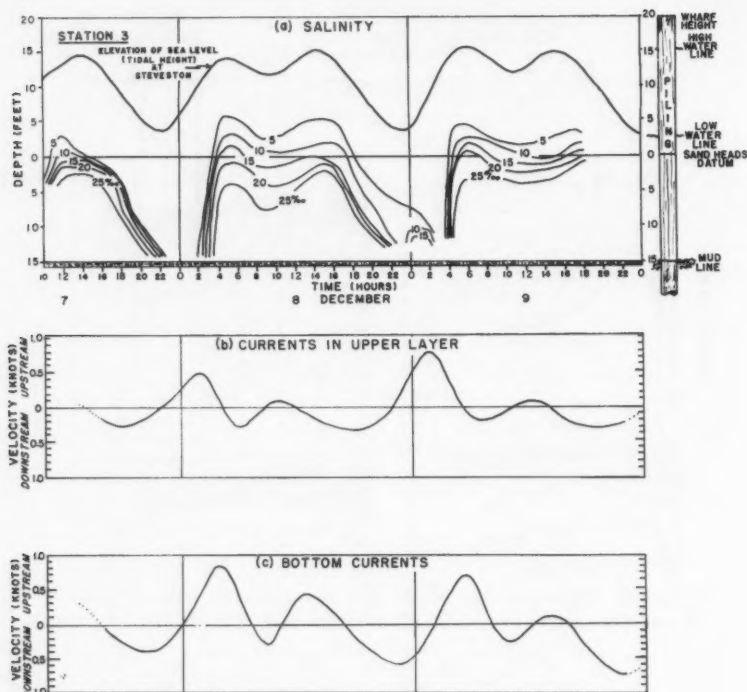


FIGURE 7. (a) Salinity and tidal heights at Station 3 in the basin showing the periods of sea water intrusion in Steveston Cannery Basin during tides of large range (river discharge = 96,000 c.f.s.),

(b) Corresponding current velocities in the upper fresh water layer, and
 (c) In the lower sea water layer.

As the sea level drops due to the falling tide in the strait, an ebb current occurs in the river. It is stronger than the flood current because of the pressure head built up by the accumulation of river water in the channel. In this case the slope of the sea level in the river is reversed, and its magnitude is approximately twice that observed during the rising tide. In the basin the ebb current in the upper layer occurs earlier than that of the sea water along the bottom.

Although the retreat of the sea water during the falling tide was only observed in the basin (Fig. 5(b,c)) it is apparent that a similar situation occurred in the channel. This has been shown by Fjarlie (1950) in the North Arm of the Fraser River.

FLUSHING OF SEA WATER IN RIVER CHANNEL AND BASIN

The degree of flushing in both the river channel and the basin is greater during the large tides than during small tides (Fig. 8). The low waters in December 1954 (Fig. 7(a)) and May 1955 (Fig. 8(c)) were similar and so were the river

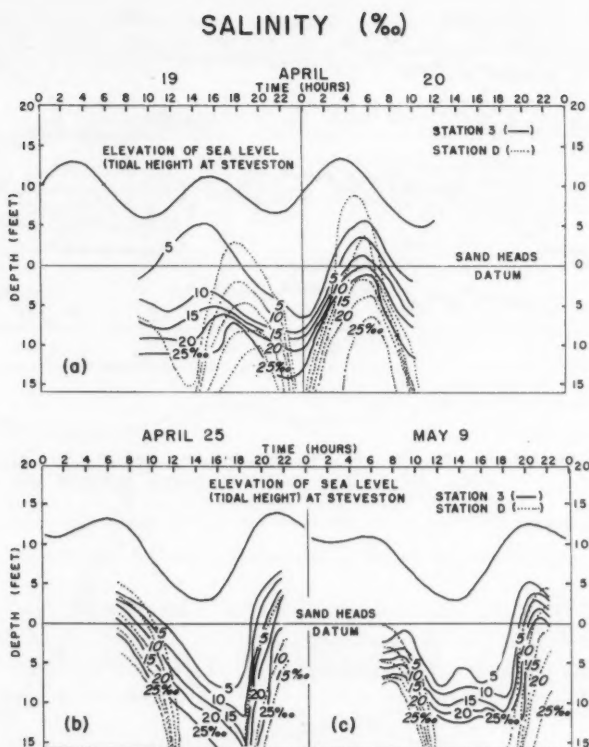


FIGURE 8. Salinity and tidal heights at Station 3 in the basin and at Station D in the main channel of the Fraser River during

- (a) Tide of small range (river discharge = 63,000 c.f.s.).
- (b) Tide of large range (river discharge = 71,000 c.f.s.).
- (c) Tide of large range (river discharge = 98,000 c.f.s.).

discharges (Fig. 9(b)); tidal ranges were 12 and 9 feet respectively. Flushing was more complete during the period of greater tidal range in December than that in May. Therefore it appears that flushing is related to the tides and more particularly to the tidal range rather than to the height of the low waters.

Except during the freshet period the main channel is flushed daily, but the basin is only partially flushed. This is probably due to the sea water in the main channel being more easily forced downstream by the river flow than that in the basin.

It is believed that the difference of flushing in the basin and the main channel cannot be attributed wholly to the difference in magnitude of the tidal currents. A factor which may also contribute to incomplete flushing of the basin is the presence of a depression lying seaward of the basin between Stations 3 and C (Fig. 3(b)). Since this depression is not in the main stream of the river, it is

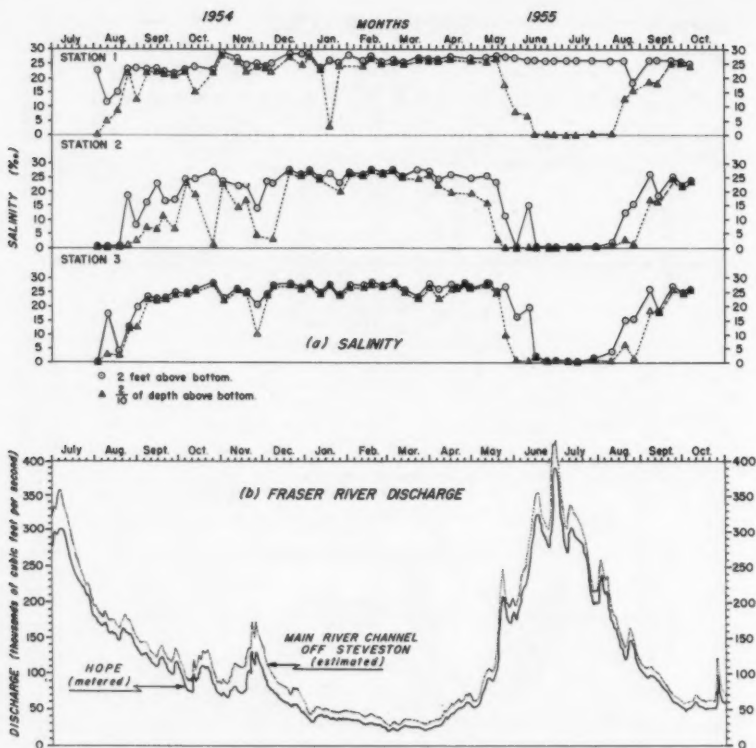


FIGURE 9. (a) Salinity of the deep water in Steveston Cannery Basin observed weekly at high tide during the period August 3, 1954, to October 30, 1955.

(b) Fraser River discharge metered daily at Hope, B.C., and estimated for daily flow off Steveston.

possible that it may retain some of the retreating sea water. The intruding water on the subsequent rising tide may force this portion of the sea water back into the basin in advance of the returning salt wedge.

Sea water was evident in the depression near the dam (Station 1) at all stages of the tide (Fig. 5). Evidently this water is not flushed during the tidal cycle. However in one series it was observed that the salinity had increased during the cycle (Fig. 5(a,b)). This suggests that the sea water had been renewed. Such renewal would occur only if the intruding sea water was more dense than the water already present. The sea water in the depression would become progressively diluted by mixing with the overlying less saline water. Renewal depends on the extent of such mixing.

There are other depressions in the basin that are smaller than the one near the dam, such as those lying between Stations 1 and 2 (Fig. 2) and at Stations *e* and *h* (Fig. 10). Any such depressions would impede the flushing of sea water

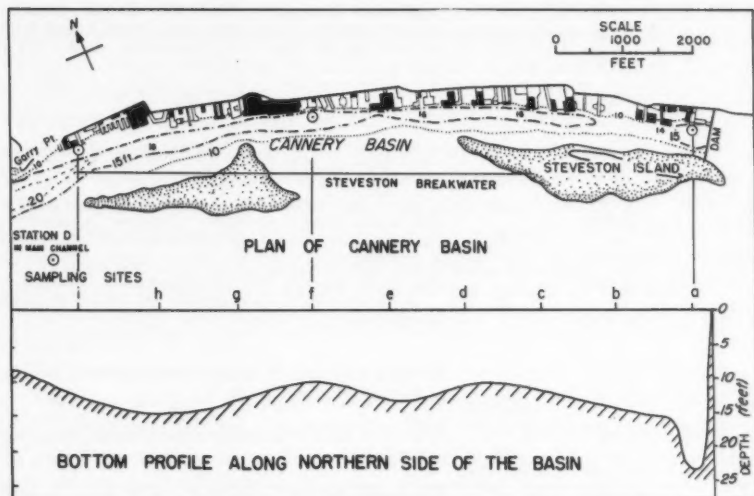


FIGURE 10. Test block sampling sites in Steveston Cannery Basin.

by forming "salt-water pools" along the bottom when the sea water in the general level is withdrawn. Flushing in these small depressions would therefore be incomplete during a tidal cycle. It is only in regions free of such depressions that adequate flushing can occur.

EFFECT OF RIVER DISCHARGE ON SEA WATER INTRUSION

In Figure 9(a) are shown the weekly observations, at high tide, of the salinity of the deep water in the basin. With the exception of the brief period of about 6 weeks during the freshet, intrusion occurred throughout the year. The bottom salinity exceeded 25‰ in most cases. The details of the relationship between intrusion and discharge are summarized in Table II. It is noted that when the discharge reached 250,000 c.f.s. most of the sea water was flushed, but not until it had attained a value as large as 300,000 c.f.s. was the basin free of sea water (except for that in the depression). Intrusion did not recommence until the discharge had dropped to 180,000 c.f.s.

The reason for this additional discharge being required to drive out the sea water is not too clear. However it seems probable that a greater discharge is required to completely flush out the sea water in the various depressions located in the main river channel. Once these are flushed out then they may remain clear at lesser discharge levels.

From the illustration of the salt wedge (Fig. 3(b)) it appears likely that the intrusion may have reached upstream as far as Woodward's Landing, about 10 nautical miles from the river mouth at river discharge of about 100,000 c.f.s. Wright (1951) observed sea water in the channel off Woodward's Landing when the discharge was 50,000 c.f.s. It is probable then, that the salt wedge

TABLE II. General relationship between sea water intrusion in Steveston Cannery Basin and Fraser River discharge, as shown by salinity of deep water at high tide (bottom 6 feet of Stations 2 and 3; bottom 9 feet at Station 1). Months are divided into three thirds: days 1-10 as I; 11-20 as II; 21-30 or 31 as III.

Dates	Discharge	Salinity	Remarks
1954	<i>c.f.s.</i>	<i>‰</i>	
III July to III August	200,000 to 150,000	0 to 18	First sign of sea water occurred (I August). Total intrusion by III August.
I Sept. to III Nov.	150,000 to 100,000	20	Sea water present in basin. Decrease in salinity corresponding to secondary maximum discharge at III November
I Dec. to III Dec.	100,000 to 50,000	25	Sea water present in basin. Remained in basin most of tidal cycle. May remain in basin throughout tidal day
1955			
I Jan. to I April	50,000	25 (max. 28)	Sea water present in basin. Likely to remain in basin throughout tidal cycle
I April to I May	50,000 to 100,000	25 (max. 28)	Sea water present in basin. Remained in basin most of tidal day
II May to III May	100,000 to 200,000	0 to 28	Sea water present in basin. Large decrease in salinity at all stations. At II May near end of intrusion but appreciable amount of sea water still remained in basin
III May to II June	200,000 to 300,000	0 to 15	Some sea water still evident but at II June basin free of sea water (except trapped water in "depression")
II June to III July	400,000 to 300,000	0	No sea water in basin (except trapped water in "depression")
III July to I August	300,000 to 250,000	0 to 3	First sign of sea water at I August
I August to I Sept.	200,000 to 100,000	0 to 28	Total intrusion at III August

may reach farther upstream than Woodward's Landing at lower discharge levels.

During periods of large discharge it may be forced downstream and at periods of very large discharge it is possible that there is little, if any, salt wedge entering the river. This probably occurred during the freshet period when the discharge was 300,000 c.f.s. or greater.

ADDITIONAL INFORMATION

TEMPERATURE. As shown in Figures 4(b) and 6, the temperature structures in the main channel and in the basin during the winter were quite similar to each other, the upper layer of fresh water having a temperature of 5°C. and the deep layer of sea water having a temperature exceeding 8°C. During severe winters sea surface temperatures may reach as low as 0°C. In summer the temperature of the basin water reaches a value as high as 18°C. (Pacific Oceanographic Group of the Fisheries Research Board of Canada, 1956). As in the salinity structure, it is fairly easy to recognize the three principal layers.

In so far as intrusion is concerned, sea water temperature is secondary to salinity since the latter has more influence on the density of the water. However, it may serve as an additional identifying characteristic for fresh and sea water when their temperatures are different. This is particularly true in the winter.

DISSOLVED OXYGEN IN THE BASIN. The concentration of dissolved oxygen (expressed as percentage of saturation) was highest at the surface (95 to 100%) and generally decreased to about 90% at a depth of 9 feet still in the upper layer. It continued to decrease and reached 75% at a depth of 18 feet in the saline water. The lowest concentration of 55% was encountered at a depth of 6 feet above the bottom in the depression, 12 feet below the general level of the basin. Oxygen concentration in the upper layer at the mouth of the river is greater than 90% (Pacific Oceanographic Group of the Fisheries Research Board of Canada, 1954).

The decrease of dissolved oxygen toward the bottom of the basin suggests that there is a demand capable of utilizing a considerable part of the available oxygen during the interval that the sea water was present in the basin. Such an appreciable oxygen demand is attributed to the cannery wastes and domestic sewage which form a black malodorous mud along the bottom.

INCIDENCE OF THE SHIPWORM, *BANKIA SETACEA* TYRON, IN STEVESTON CANNERY BASIN

METHODS AND RESULTS

The initial oceanographic observations of salinity (August to December 1954) and temperature (December 1954) indicated that the conditions in the basin were tolerable for *Bankia*. The next step was to determine whether or not *Bankia* settlement occurred.

Incidence of *Bankia setacea* larvae was investigated by suspending blocks of wood at representative sites in the basin (positions *a* to *i* in Fig. 10). The blocks cut from green Douglas fir, offered 16 square inches of surface area to settling larvae. These blocks were suspended at five levels, 2, 4, 6, 8 and 12 feet above the bottom (mudline). Initially, only five sites were chosen for setting out the blocks. However, with the discovery of *Bankia* settlement in the basin the number of sites was increased to nine. After the blocks had been exposed for one month in the water, they were examined for larval settlement (Fig. 11). A new set of blocks was inserted to replace the old ones. These monthly observations were carried out from December 1954 to November 1955. They included all tidal ranges and all levels of river discharges.

Bankia settlement was observed at only three stations. It occurred in the bottom blocks at Stations *e* and *h* and in all the blocks at Station *a* (Table III). At Stations *e* and *h* the settlement was sporadic, occurring only three times during the course of the year. In contrast, larval settlement occurred at Station *a* at the bottom three levels during every month except during the freshets in June and July. (Although blocks from Station *a* during March 4 to May 6, 1955, are missing, it is likely that settlement occurred during these months.)

TABLE III. Counts of *Bankia setacea* (number per square foot) settling in test blocks in Steveston Cannery Basin at various heights above the bottom. Station *j* is in the main river channel near Station D (Fig. 3).

Sampling sites:		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	<i>i</i>	<i>j</i>
Depth of water at zero tide datum (feet):		23	15	12	10	13	10	13	16	12	30
Dates	Height										
	<i>feet</i>										
1954-55 Dec. 9-Jan. 18	12	0	0	0	0	...
	8	0	0	0	0	...
	6	9	0	0	0	...
	4	54	0	0	0	...
	2	45	0	81	0	...
Dec. 9-Mar. 4	12	0	0	0	0	...
	8	18	0	0	0	...
	6	27	0	0	0	...
	4	81	0	0	0	...
	2	90	27	288	0	...
1955 Mar. 4-May 6	12	0	0	0	...
	8	0	0	0	...
	6	0	0	0	...
	4	0	0	0	...
	2	0	0	0	...
May 6-June 12	12	0	0	0	0	0	0	0	0	0	...
	8	27	0	0	0	0	0	0	0	0	...
	6	54	0	0	0	...	0	0	0
	4	90	0	0	0	...	0	0	0
	2	135	0	0	0	...	0	0	0
June 12-July 16	12	0	0	0	0	0	0	0	0	0	...
	8	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	...
July 8-Aug. 10	12	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0
Aug. 10-Sept. 12	12	0	0	0	0	0	0	0	0	0	0
	8	72	0	0	0	0	0	0	0	0	0
	6	144	0	0	0	0	0	0	0	0	0
	4	315	0	0	0	0	0	0	0	0	0
	2	549	0	0	0	0	0	0	45	0	0
Sept. 12-Nov. 8	12	612	0	0	0	0	0	0	0	0	0
	8	783	0	0	0	0	0	0	0	0	0
	6	1,197	0	0	0	0	0	0	0	0	0
	4	1,044	0	0	0	0	0	0	0	0	0
	2	1,899	0	0	0	0	0	0	0	0	0
Total settlement for 11 months	12	612	0	0	0	0	0	0	0	0	0
	8	900	0	0	0	0	0	0	0	0	0
	6	1,431	0	0	0	0	0	0	0	0	0
	4	1,584	0	0	0	0	0	0	0	0	0
	2	2,718	0	0	0	27	0	0	414	0	0

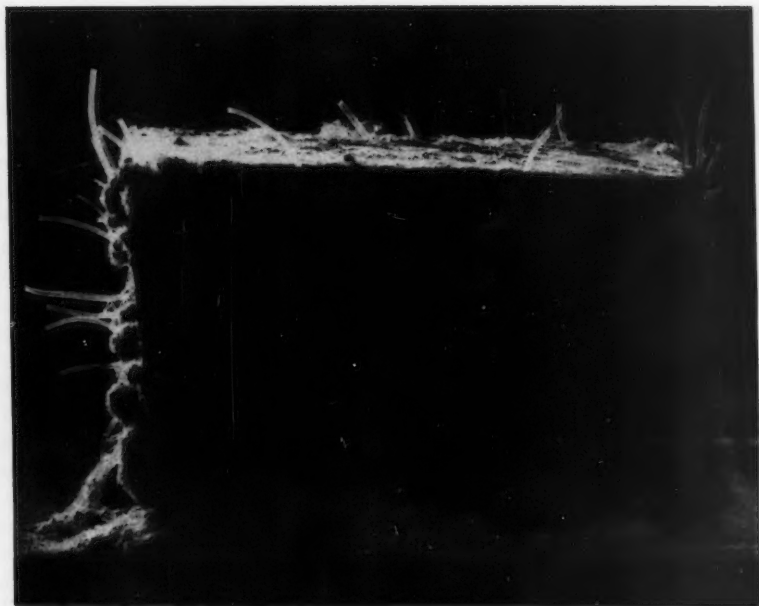


FIGURE 11. Underwater photograph of *Bankia* infested test block, showing siphons ($\times 1$).

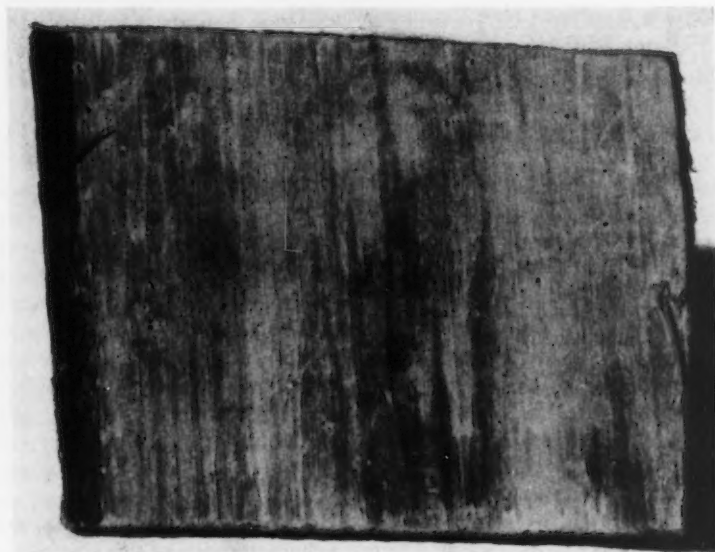


FIGURE 12. Photograph of the sanded surface of a *Bankia* infested test block ($\times 1.2$).

At this location the blocks at the 8-foot level above the bottom were attacked intermittently and the blocks at the 12-foot level only once. With the exception of the examinations during June and July, each new observation showed an increase in the incidence of *Bankia* per unit area. No larval settlement was observed in the upper blocks where the salinity was always less than 15‰.

With the discovery of *Bankia* in the basin, it remained to be established whether or not they survived and grew to maturity. In order to determine this, blocks known to contain at least six juvenile *Bankia* each were obtained from Massett Inlet in northern British Columbia and set out in the basin in the same manner as the uninfested test blocks. A similar group of infested blocks was kept in Departure Bay in Nanaimo, as a control. Here the mean salinity exceeded 23‰. Both the test and control blocks were left in the water for 12 weeks and then examined for live individuals (Fig. 12).

Most of the *Bankia* died soon after being placed in Steveston Cannery Basin (Table IV). Surviving *Bankia* were found only in the blocks at the 2- and 4-foot levels at Station *a* in the depression at the head of the basin (blocks at 8-foot level at Station *a* were missing) and in the control blocks in Departure Bay. Growth in length was determined by peeling away successive layers of wood and measuring the extent of the burrows (Fig. 13). Evidence of slight growth was noted for specimens at Stations *a*, *e* and *h*. In the bottom blocks at the latter two stations, the *Bankia* had grown 1/16 inch before dying, while at the 6-foot level at Station *a* they had grown to 1/2 inch before dying. The surviving *Bankia* grew to one inch in Steveston Cannery Basin and 3 inches in Departure Bay. During the 12-week period, the lowest salinity encountered by the living *Bankia* at both locations was 20‰.

TABLE IV. Length in inches of *Bankia setacea* in infested blocks from August 4 to November 8 at various heights above the bottom. (Original length of *Bankia* = 1/16 inch. All *Bankia* were dead when recovered except those at 2 and 4 feet, Station *a*. *Bankia* in test blocks on the bottom at Departure Bay grew 1 to 3 inches in same time.)

Stations	Height above the bottom (feet):				
	2	4	6	8	12
	inch	inch	inch	inch	inch
<i>a</i>	1	1	1/8-1/2	...	1/16
<i>b</i>	1/16	1/16	1/16	1/16	1/16
<i>c</i>	1/16	none	1/16	1/16	1/16
<i>d</i>	1/16	1/16	1/16	1/16	1/16
<i>e</i>	1/8	1/8	1/16	1/16	1/16
<i>f</i>	1/16	1/16	1/16	1/16	1/16
<i>g</i>	1/16	1/16	1/16	1/16	1/16
<i>h</i>	1/16-1/8	1/16-1/8	1/16-1/8	1/16	1/16
<i>j</i>	1/16	1/16	1/16	1/16	1/16

DISCUSSION

The present status of *Bankia setacea* in British Columbia has recently been reviewed by Quayle (1956b). The main characteristics of this species according to him are:

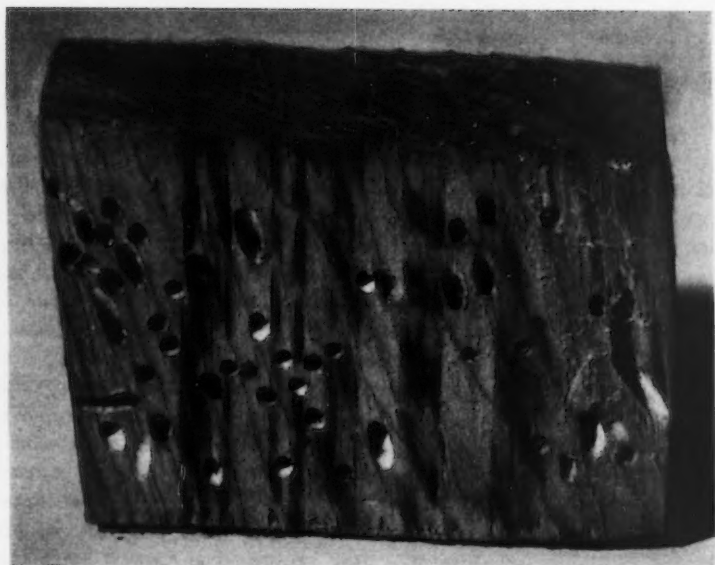


FIGURE 13. Photograph of Figure 12 after $\frac{1}{4}$ inch of surface cut away ($\times 1.2$).

1. It is distributed by the water currents during a planktonic larval stage of about a month.
2. It matures early and is capable of spawning in 4 months. It can breed at any time of the year.
3. It is tolerant to widely varying environmental conditions of salinity, temperature, current velocity, and abundance of food.
4. Its attack on wooden structures is most concentrated just above the bottom (mudline).

Members of the *Teredo* family can survive on wood alone (Horonjeff and Patrick, 1952). Hence the abundance of its main source of food, plankton, may not be a limiting factor. For *Teredo*, the time of breeding is reported to be influenced by the water temperature. However for *Bankia*, which is a member of the same family, the close relationship between breeding and temperature has not been shown (Quayle, 1956b). In British Columbia waters, *Bankia* is known to breed with varying intensity throughout the year. It has occurred in waters of relatively high salinity (28.5 to 30.6‰). Maximum infestation has been reported for conditions of range of surface temperature 4 to 16°C. and range of salinity 5 to 22‰ (Black and Elsey, 1948). Unfortunately, observations of temperature and salinity at the bottom (mudline), where infestation is most intense, are lacking. However, in a recent experiment in the laboratory, *Bankia* exposed to low salinity water failed to survive after 6 days in water of salinity 8‰ and at temperature 13°C. (Fig. 14, adapted from figure 3, Trussell *et al.*, 1956).

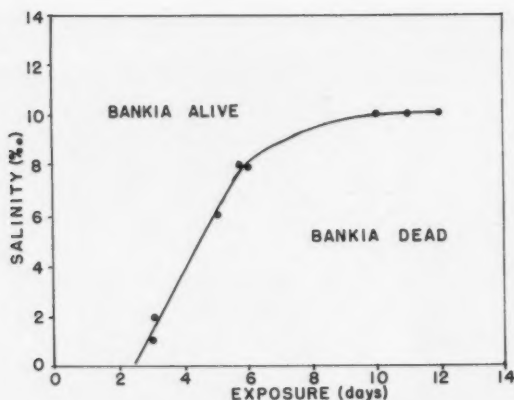


FIGURE 14. Relationship of salinity and exposure to survival of *Bankia*. The area above the line describes the conditions to which *Bankia* is tolerant. The line describes the incipient level at which mortality of *Bankia* just begins and is a function of length of exposure. The area below the line describes lethality. (Adapted from figure 3, Trussell *et al.*, 1956.)

The salinity and temperature (Fig. 6, 9(a)) of the intruded sea water in the basin were similar to those of water at other localities (Black and Elsey, 1948) where *Bankia* infestation had occurred. Currents along the bottom did not exceed 0.8 knot (Fig. 7(c)). Soundings made along the edge of the wharves revealed depressions along the bottom (Fig. 10). As mentioned earlier the intruded sea water would not be adequately flushed out of the depressions during a tidal cycle and therefore sea water would tend to remain longer in such depressions than in the rest of the basin. In the extreme case, as in the large depression at Station *a*, sea water is virtually trapped (Fig. 10—the depression shown at Station *a* in Fig. 10 is part of that shown at Station 1 in Fig. 2).

On the basis of bottom topography and oceanographic conditions, the basin can be divided into three types of environmental regions:

1. Those where the sea water is flushed regularly, i.e., oceanographic Station 1 (Fig. 2) and *Bankia* test Stations *b*, *c*, *d*, *f*, *g*, and *i* (Fig. 10).
2. Those where sea water is only occasionally flushed, i.e., *Bankia* test Stations *e* and *h* (Fig. 10).
3. Those where the sea water is held almost indefinitely, i.e., oceanographic Station 1 (Fig. 2) and *Bankia* test Station *a* (Fig. 10).

While the conditions affecting the activity of adult *Bankia* have received considerable attention, the conditions affecting the larval stages have received only cursory examination. Larvae were reported to settle in sea water of salinity 5‰ (Black and Elsey, 1948) but the observers failed to note whether the animals continued to survive. In Steveston Cannery Basin the larvae settled in sea

water of salinity as low as 15‰ but failed to survive where the salinity was less than 20‰.

In a log storage basin at the mouth of the Fraser River, conditions suitable for adult *Bankia* were reported but no larvae were observed to settle (Trussell *et al.*, 1956). Experiments with *Teredo* larvae revealed that maximum settlement takes place in water of current velocities less than 0.5 knot and that virtually no settlement takes place when currents exceed 2 knots (Horonjeff and Patrick, 1952). Suitable conditions for larval settlement in Steveston Cannery Basin occurred along the bottom at each sampling site for almost three-quarters of the day during tides of large range and even longer during tides of small range (Fig. 7 and 8—salinity greater than 15‰ and current less than 0.8 knot). However, settlement occurred at only Stations *a*, *e*, and *h*. Each of these stations was in a depression. The presence of the depression may thus contribute to the success of larval settlement. From this point of view the most important feature of the depressions, besides providing more time for the larvae to encounter a wood substratum, was the maintenance of an environment to which the animal had become adapted by the retention of intruded sea water. The importance of this feature was demonstrated by comparing the survival and growth of *Bankia* introduced into the three types of environmental regions described earlier. Where the sea water was flushed regularly, the animals died almost immediately. Where the sea water was inadequately flushed as at Stations *e* and *h* (Fig. 10) some growth was noted but the *Bankia* failed to survive for more than a few days. Where the sea water was trapped as at Station *a* (Fig. 10) growth was noted and the *Bankia* were alive after 12 weeks in sea water of salinity 20‰.

Quayle (1956a) reported an average growth rate of 2.8 inches per month during the winter and 6 inches per month during the summer for *Bankia* in Ladysmith Harbour. He associated the increase in growth rate in summer with the higher water temperatures prevalent in that season. In comparison, the *Bankia* kept in Departure Bay during the late summer grew 1 inch per month and those in Steveston Cannery Basin, $\frac{1}{3}$ inch per month. The lower growth rate found in the present experiment may have resulted in part from the effect of transplanting *Bankia* from northern British Columbia waters to southern British Columbia waters. Also, water temperatures in summer are higher in Ladysmith Harbour than in Departure Bay or Steveston Cannery Basin and it may be presumed that this engendered a greater growth rate. Undoubtedly differences in other environmental conditions such as abundance of food may also occur between these localities.

Bankia have been reported to mature 4 months after settlement (Quayle, 1956b). Station *a* (Fig. 10) is the only location in Steveston Cannery Basin where conditions were suitable for the animal to grow to maturity. Here, indigenous spawning could have occurred as early as May in 1955. However, the absence of larval settlement in June and July suggests that a mature population had not become established in the basin at that time. The tenfold increase in settlement during September and October (Table III) seems to have been the result of indigenous spawning. Further indications of local spawning at this time

were found in the occurrence of larvae at the 12-foot level and their absence from Stations *c* and *h*.

CONCLUSIONS

On the basis of these oceanographic and biological findings it seems possible to remove the present population of *Bankia* and prevent any future attack. Several methods of control are available but only one seems practical, namely dredging the basin on a uniform slope and filling all depressions. This would eliminate the "salt-water pool" where sea water could lie during periods of flushing such as the bottom 8 feet at Station *a*, and below 15 feet at Station *h*. The cross-section of this basin should have a round bottom, and lengthwise it should slope from a minimum of 15 feet depth at the head to a maximum of about 20 feet at the mouth of the basin. It is necessary that this dredged portion continue with increasing depth through the river to the sea. There should be no depressions or cross-channel bars seaward of the basin. In particular, the depression lying seaward of the mouth of the basin between Stations 3 and *c* should be eliminated.

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